Zhao *et al. Avian Res (2017) 8:10*
DOI 10.1186/s40657-017-0068-3

Avian Research

RESEARCH

Open Access

Do migrant and resident species differ in the timing of increases in reproductive and thyroid hormone secretion and body mass? A case study in the comparison of pre-breeding physiological rhythms in the Eurasian Skylark and Asian Short-toed Lark

Lidan Zhao[1], Lijun Gao[1], Wenyu Yang[1], Xianglong Xu[1], Weiwei Wang[1], Wei Liang[2] and Shuping Zhang[1*]

Abstract

Background: Physiological preparation for reproduction in small passerines involves the increased secretion of reproductive hormones, elevation of the metabolic rate and energy storage, all of which are essential for reproduction. However, it is unclear whether the timing of the physiological processes involved is the same in resident and migrant species that breed in the same area. To answer this question, we compared temporal variation in the plasma concentration of luteinizing hormone (LH), testosterone (T), estradiol (E_2), triiothyronine (T_3) and body mass, between a migrant species, the Eurasian Skylark (*Alauda arvensis*) and a resident species, the Asian Short-toed Lark (*Calandrella cheleensis*), both of which breed in northeastern Inner Mongolia, China, during the 2014 and 2015 breeding seasons.

Methods: Twenty adult Eurasian Skylarks and twenty Asian Short-toed Larks were captured on March 15, 2014 and 2015 and housed in out-door aviaries. Plasma LH, T (males), E_2 (females), T_3 and the body mass of each bird were measured every six days from March 25 to May 6.

Results: With the exception of T, which peaked earlier in the Asian Short-toed Lark in 2014, plasma concentrations of LH, T, E_2 andT_3 of both species peaked at almost the same time. However, Asian Short-toed Larks attained peak body mass earlier than Eurasian Skylarks. Plasma T_3 concentrations peaked 12 days earlier than plasma LH in both species. Generally, plasma LH, T, E_2, T_3 and body mass, peaked earlier in both species in 2014 than 2015.

Conclusions: The timing of pre-reproductive changes in the endocrine system and energy metabolism can be the same in migrant and resident species; however, residents may accumulate energy reserves faster than migrants. Although migration does not affect the timing of pre-breeding reproductive and metabolic changes, migrant species may need more time to increase their body mass. T levels in resident species may be accelerated by higher spring temperatures that may also advance the pre-breeding preparation of both migrants and residents.

Keywords: *Alauda arvensis*, *Calandrella cheleensis*, Pre-breeding, Physiological preparation, Migratory birds

*Correspondence: zhangshuping@muc.edu.cn
[1] College of Life and Environment Sciences, Minzu University of China, Beijing 100081, China
Full list of author information is available at the end of the article

Background

Reproduction is one of the most energetically demanding activities in the life of birds. At mid and high latitudes, suitable conditions for breeding are relatively brief and birds that live at these latitudes must therefore time their reproductive activity to coincide with periods when food suitable for the survival of parents and offspring is relatively abundant (Dawson et al. 2001). Birds must complete three stages of physiological preparation to begin breeding. First, the hypothalamic-pituitary–gonadal axis (HPG) is activated. The hypothalamus secrets the gonadotrophin-releasing hormone cGnRH-I when stimulated by the longer days of early spring (Yasuo and Yoshimura 2009). This hormone is then transported in the blood to the pituitary where it stimulates the secretion of the luteinizing hormone (LH) and the follicle-stimulating hormone (FSH). LH and FSH induce development of the ovaries or testes, which then regulate the production of the sex hormones, mainly estradiol (E_2) and testosterone (T) will enter the circulation to start the reproductive behavior (Aurélie et al. 2010). Secondly, birds must increase their metabolic rate in preparation for higher energy consumption during breeding (Ricklefs 1974; Carey 1996; Nilsson and Raberg 2001). Pre-reproductive energy metabolism is an important factor affecting the timing of breeding (Stevenson and Bryant 2000). Thyroid hormones, especially triiothyronine (T_3), play an important role in substrate metabolism and thermogenesis, and T_3 plasma concentration is positively correlated with BMR (basic metabolic rate) (Yen 2001; Chastel et al. 2003; Li et al. 2010; Welcker et al. 2013; Zheng et al. 2013). Plasma T_3 levels are known to increase before breeding in several bird species (Smith 1982; Pathak and Chandola 1983). It has also been found that individual birds that increase their plasma T_3 levels sooner start breeding earlier (Chastel et al. 2003). Thirdly, after going through a period of relative food shortage in the winter, or depleting their energy reserves during migration, birds have to increase their food intake before breeding in order to meet the increased nutritional requirements of the breeding season (Hegemann et al. 2012). Body mass, which can be regarded as the balance between energy intake and its expenditure (Zhao et al. 2015) usually increases before breeding (Wang and Lei 2011; Hegemann et al. 2012).

Migratory species must compete with residents for breeding resources, including territories and food, after their arrival at the breeding grounds. However, unlike resident birds, migratory birds consume a large amount of energy in the course of migrating to the breeding grounds (Jenni et al. 2000). Therefore migratory species might attain breeding condition later than residents for their migration energy consumption. They would therefore be expected to be at a disadvantage in subsequent competition for breeding resources (Morbey and Ydenberg 2001). Because the duration of physiological preparation for breeding determines the timing of reproduction, it is important to determine if the timing of the physiological processes involved in activation of the reproduction endocrine system and, at the same time, increasing their metabolic rate and energy storage is the same in migratory and resident species. To the best of our knowledge, no one has yet conducted the necessary research to address this question in wild birds.

In our study, we compared the timing of physiological preparation for breeding in two members of the Alaudidae, the Eurasian Skylark (*Alauda arvensis*) and the Asian Short-toed Lark (*Calandrella cheleensis*), both of which breed in the grasslands of northeastern Inner Mongolia, China. The Eurasian Skylark is a migratory species that arrives at the Inner Mongolian grasslands in early March and begins nesting in mid-April (Lou 1966). The Asian Short-toed Lark is a resident that also starts breeding in mid-April. The breeding periods of the two species are therefore highly synchronous, with the main food of nestlings of both species as grasshopper nymphs which are only seasonally abundant on the grasslands in the breeding season (Tian et al. 2015). In order to compare the timing of physiological preparation of the reproductive endocrine system, energy metabolism and energy storage in these two species, we compared their pre-breeding temporal trends in LH, T, E2 and T3, plasma concentrations and body mass during the spring of 2014 and 2015. We hypothesize that migratory and non-migratory birds will show differences in elevating LH, T, E_2 and T_3 levels and body mass.

Methods

Study area

Our study site was in the Dalai National Nature Reserve (47°45′50″–49°20′20″N; 116°50′10″–118°10′10″E), located in the northeastern part of Inner Mongolia, China. This is a semiarid, steppe region where the mean annual temperature is −0.6 °C, with 283 mm precipitation and a potential evaporation of 1754 mm. The dominant plant species are *Stipa krylovii*, *Leymus chinesis* and *Cleistogenes squarrosa*. Winters are longer than summers and the approximate average maximum daytime temperature is −20.02 °C in January and 22.72 °C in July.

Study design

Twenty adult Eurasian Skylarks and twenty adult Asian Short-toed Larks (sex ratio = 1:1) per year were captured in mist-nets on the same date, March 15, in 2014 and 2015. Birds were housed in out-door aviaries (50 cm × 40 cm × 35 cm) (one bird per aviary), in which they were acclimatized to captivity for 10 days. Birds were fed mixed seeds, boiled eggs, mealworms and provided with water during this period. At least 100 μL of whole blood was collected from each bird every four days from March 25 to May 6 in 2014 and 2015. Blood was collected into heparinized micro-capillary tubes within 1–3 min of capture by puncturing a brachial wing vein with a disinfected 23G needle. The skin around the puncture site was disinfected with medical alcohol before and after puncturing. Pressure was applied to the puncture site for 1 min with an alcohol-soaked cotton wool swab to stop bleeding immediately after blood samples had been collected. Blood samples were stored at 4 °C for up to 8 h until centrifuged at 3000 r/min for 10 min. The resultant blood plasma and cells were separated into different micro-centrifuge tubes and then kept frozen until assayed. The blood plasma samples were used for hormone assay, while the blood cells were used to extract DNA for molecular sex discrimination based on methods described by Griffiths et al. (1996). We also considered the ambient temperature effect on the difference between the two study years. Daily maximum and minimum temperature data in March and April of our study site were obtained from the Inner Mongolian Meteorological Bureau (http://www.nmgqxfw.com/).

Hormone assays and measurement of body mass

Plasma LH, T, E_2 and T_3 levels were measured using chicken enzyme immunoassay kits from MyBioSource (cat#MBS165746), Assay Design (cat #ADI-901-065 and -174) and Cygnus (cat # KL023681), respectively. In order to confirm that these kits would work on the plasma of the two lark species we first used the kits to analyze the concentration-dependent binding dynamics of diluted plasma samples from 20 birds of each species. These samples had been pooled and diluted by 1, 1/2, 1/4, 1/8, 1/16 and 1/32, according to the methods used by Chastel et al. (2005) and Washburn et al. (2007). The resulting LH, T and E_2 dilution curves obtained for each species closely approximated the standard ELISA Kit curves, confirming that the kits could reliably assess plasma LH, T, E_2 and T_3 levels in both species. Body mass was measured with a spring balance (PESOLA200060, Germany). For the Asian Short-toed Lark, the inter- and intra-plate coefficients of variation for LH were 7.06 and 6.5%, for T 9.1 and 7.7% and 8.5 and 2.4% for E_2. For the Eurasian Skylark, the inter- and intra-plate coefficients of variation for LH were 7.12 and 6.3%, for T 8.7 and 7.4% and 8.1 and 2.01% for E_2.

Data analysis

We used Linear Mixed Models (LMMs) to determine the effects of sex, sample date and species on LH, T_3, as well as body mass in each of the two years. Sex, sample date, species and their interactions between these factors, were modeled as fixed factors with individual bird as a random factor. The LMMs were also used to determine the effects of sample date and species on T and E_2 in both years. Sample date, species and the interactions between these factors were modeled as fixed factors, again with individual bird as a random factor. The response variables LH, T, E_2 and T_3 and body mass were first logarithmically transformed to correct for departures from normality and homogeneity of variance. If there was no significant difference between males and females of each species in a given variable based on the results of LMMs, then the relevant data from each sex were pooled for analysis, otherwise data from males and females were analyzed separately. Repeated measure ANOVA was used to analyze the difference between males and females when the variable "sex" showed significant effects in the LMMs. Finally, we used the dates on which peak plasma LH, T, E_2, T_3 concentrations and body mass were recorded as indicators of the speed of pre-breeding physiological preparation in both species.

Results

Temperature difference between 2014 and 2015

Mean daily maximum and minimum ambient temperatures in March and April in 2014 and 2015 are shown in Fig. 1. Both March and April daily maximum temperatures were significantly higher in 2014 than in 2015.

Reproductive hormones

Because there were no significant differences in LH levels between males and females of either species in both years of the study (Table 1), LH data from each sex were pooled for subsequent analyses. The LMMs indicated that

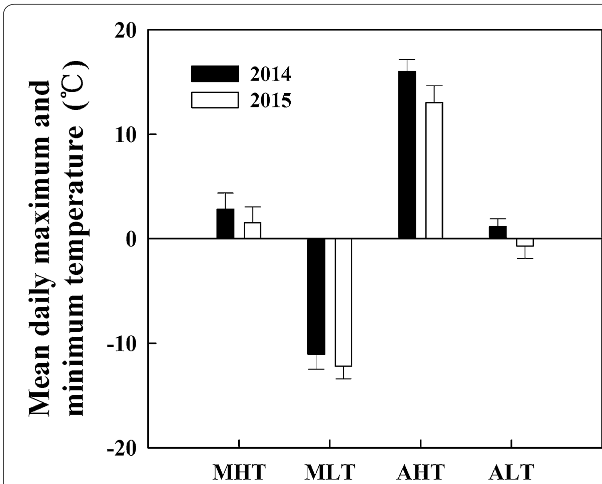

Fig. 1 Mean daily maximum and minimum temperatures in the Dalai National Nature Reserve, Inner Mongolia, China, in March and April 2014 and 2015. *MHT* March highest temperature, *MLT* March lowest temperature, *AHT* April highest temperature, *ALT* April lowest temperature. The average temperature of March and April in 2014 were higher than in 2015

Table 1 Results of a linear mixed model of the effects of species, time and sex on plasma LH and T_3 and body mass in Asian Short-toed Larks and Eurasian Skylarks in 2014 and 2015

Year	Response variable	Explanatory variable	F	p
2014	LH	Species	3.32	*<0.05*
		Sample date	13.96	*<0.01*
		Sex	0.50	0.48
		Species * sample date	0.05	1.00
		Species * sex	1.30	0.26
		Sample date * sex	0.47	0.76
		Species * sample date * sex	0.48	0.75
	T	Species	4.86	*<0.05*
		Sample date	6.85	*<0.01*
		Species * sample date	0.81	0.50
	E_2	Species	0.00	0.95
		Sample date	7.63	*<0.01*
		Species * sample date	0.20	0.90
	T_3	Species	15.52	*<0.01*
		Sample date	4.50	*<0.01*
		Sex	0.88	0.35
		Species * sample date	0.58	0.68
		Species * sex	0.72	0.40
		Sample date * sex	0.46	0.77
		Species * sample date * sex	0.12	0.98
	Body mass	Species	1918.50	*<0.01*
		Sample date	22.25	*<0.01*
		Sex	8.44	*<0.01*
		Species * sample date	3.32	*<0.01*
		Species * sex	22.63	*<0.01*
		Sample date * sex	0.42	0.87
		Species * sample date * sex	0.64	0.70
2015	LH	Species	4.30	*<0.05*
		Sample date	14.92	*<0.01*
		Sex	3.39	0.07
		Species * sample date	1.09	0.37
		Species * sex	1.13	0.29
		Sample date * sex	0.56	0.71
		Species * sample date * sex	1.03	0.39
	T	Species	1.13	0.29
		Sample date	4.22	*<0.01*
		Species * sample date	0.49	0.76
	E_2	Species	2.96	0.09
		Sample date	3.00	*<0.05*
		Species * sample date	0.15	0.96
	T_3	Species	20.94	*<0.01*
		Sample date	6.24	*<0.01*
		Sex	0.55	0.46
		Species * sample date	1.33	0.7
		Species * sex	0.56	0.48
		Sample date * sex	0.34	0.89
		Species * sample date * sex	3.83	*<0.01*
	Body mass	Species	1792.43	*<0.01*
		Sample date	45.30	*<0.01*
		Sex	0.81	0.37
		Species * sample date	9.60	*<0.01*
		Species * sex	3.70	0.06
		Sample date * sex	2.78	*<0.05*
		Species * sample date * sex	1.26	0.28

All Asian Short-toed Larks and Eurasian Skylarks had been captured in the wild and sampled while held in captivity in 2014 and 2015. Data are presented as mean ± SE; italic values expressed probabilities indicate statistically significant differences

sampling date and species significantly affect the plasma LH, T and E_2 concentrations in both years (Table 1). Generally, LH, T and E_2 levels first increased, then decreased (Figs. 2, 3, 4). Mean LH levels in both species peaked on April 12th in 2014 and on April 18th in 2015 (Fig. 2). In 2014, mean plasma T levels of Asian Short-toed Larks peaked on April 18th, whereas those of Eurasian Skylarks peaked on April 24th (Fig. 3). In 2015, mean plasma T levels of both species peaked on April 24th (Fig. 3). The mean plasma E_2 levels of both species peaked on April 18th in 2014 and on April 30th in 2015 (Fig. 4).

Thyroid hormone

The results of LMMs also show that sample date and species significantly affect the plasma T_3 concentration in both years (Table 1). The mean plasma T_3 concentration of each species is shown in Fig. 5. Generally, T_3 levels first increased, then decreased. Mean T_3 levels of each species peaked on March 31st in 2014 and on April 6th in 2015 (Fig. 5). Plasma T_3 levels peaked 12 days earlier than plasma LH in both species.

Body mass

The results of LMMs show that sex, sample date and species significantly affect the body mass in both years (Table 1). Significant sexual dimorphism in body mass was detected in the Eurasian Skylark in 2014: females had significantly higher body mass than males (Repeated measure ANOVA, $F_{1,47} = 8.00$, $p < 0.01$). Body mass in both species first increased, then decreased (Fig. 6). In 2014, the mean body mass of Asian Short-toed Larks peaked on April 12th, whereas that of male and female

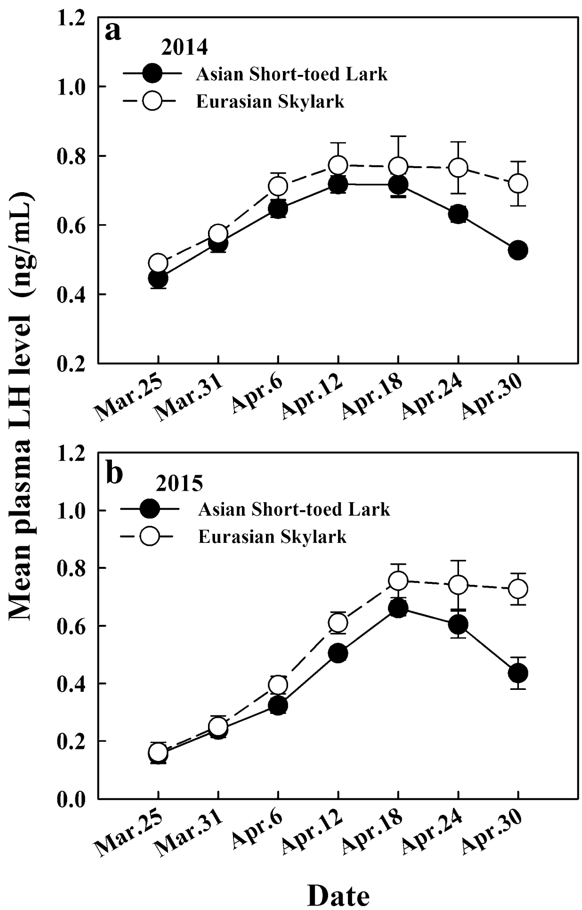

Fig. 2 Temporal trends in mean plasma luteinizing hormone (LH) levels in Asian Short-toed Larks and Eurasian Skylarks. All Asian Short-toed Larks and Eurasian Skylarks had been captured in the wild and sampled while held in captivity in 2014 (**a**) and 2015 (**b**)

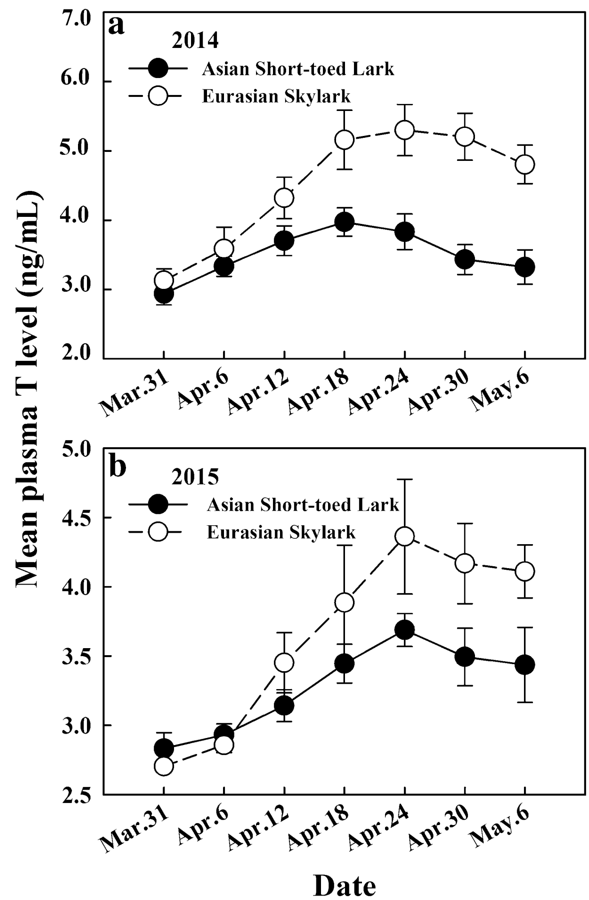

Fig. 3 Temporal trends in plasma testosterone (T) levels in Asian Short-toed Larks and Eurasian Skylarks. All Asian Short-toed Larks and Eurasian Skylarks had been captured in the wild and sampled while held in captivity in 2014 (**a**) and 2015 (**b**)

Eurasian Skylarks peaked on April 18th (Fig. 6). In 2015, the body mass of Asian Short-toed Larks peak on April 18th, whereas that of male and female Eurasian Skylarks peaked on April 24th (Fig. 6). The Asian Short-toed Larks attained peak body mass six days earlier than the Eurasian Skylarks in both years.

In general, plasma LH, T, E_2, T_3 levels, and body mass, peaked earlier in 2014 than in 2015 in both species.

Discussion

Changes of reproductive hormones

Seasonally breeding songbirds typically have an annual, reproductive endocrine cycle (Dawson et al. 2001). Briefly, as spring approaches and day length increases, secretion of GnRH and gonadotropins increases (LH and FSH) which stimulates gonadal growth leading to an increase in plasma concentrations of sex hormones. Our results show that temporal trends in LH, T and E_2 levels in wild Eurasian Skylarks and Asian Short-toed Larks follow this general pattern. The differences in the concentrations of these hormones between the two species should be explained as species specific features.

In both 2014 and 2015 plasma LH levels in both species began to rise at the end of March and peaked in the middle of April, then gradually decreased. In European Blackbirds (*Turdus merula*) (Dominoni et al. 2015), Abert's Towhee (*Pipilo aberti*) (Davies et al. 2015) and Dark-eyed Juncos (*Junco hyemalis*) (Greives et al. 2016), plasma LH levels were higher in birds that bred earlier than in those that bred later (Dawson 2008). Our results suggest that the plasma LH levels of the migratory Eurasian Skylark and resident Asian Short-toed Lark peak at the same time in the spring, suggesting that both species activate the HPG axis at the same time.

Because testosterone stimulates territorial behavior, courtship and mating in male birds, increases in plasma T concentrations are an important indicator that males are preparing to breed (Wingfield et al. 2001; Jodie et al.

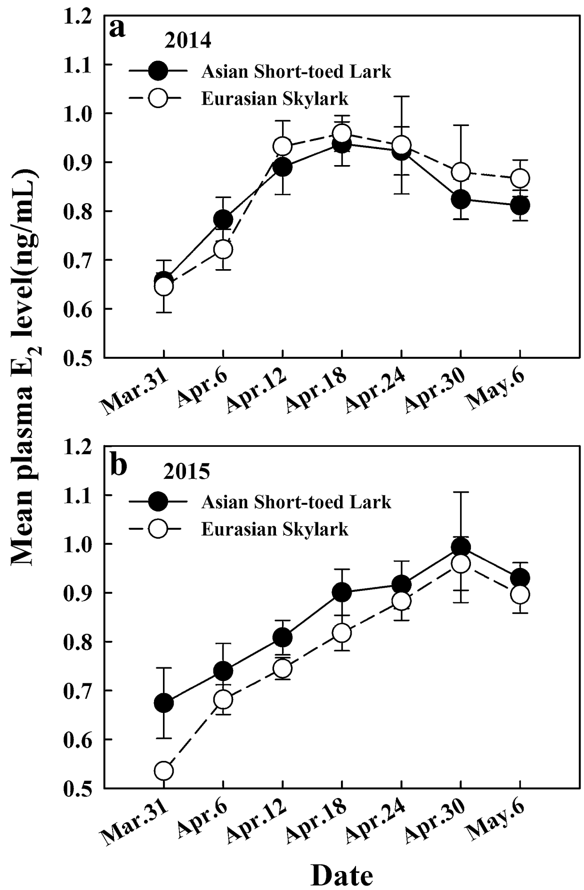

Fig. 4 Temporal trends in plasma estradiol (E_2) levels in wild Asian Short-toed Larks and Eurasian Skylarks. All Asian Short-toed Larks and Eurasian Skylarks had been captured in the wild and sampled while held in captivity in 2014 (**a**) and 2015 (**b**)

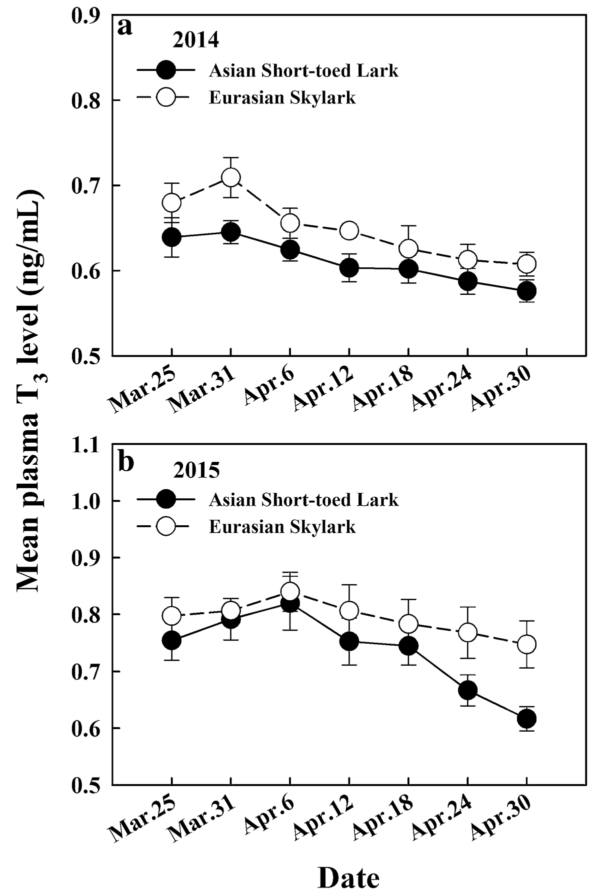

Fig. 5 Temporal trends in plasma triiothyronine (T_3) levels in wild Asian Short-toed Larks and Eurasian Skylarks. All Asian Short-toed Larks and Eurasian Skylarks had been captured in the wild and sampled while held in captivity in 2014 (**a**) and 2015 (**b**)

2007; Garamszegi et al. 2008; McGlothlin and Ketterson 2008; Tonra et al. 2011). Our results show that plasma T concentrations peaked earlier in the Asian Short-toed Lark than in the Eurasian Skylark in 2014, but at the same time in 2015. This difference may be due to the warmer early spring (March and April) temperatures recorded in 2014. The average March temperature in 2014 was 1.5 °C and in April 3 °C, higher than those in 2015. Higher spring temperatures have been found to accelerate testis maturation in male birds (Silverin et al. 2008). Resident birds are more sensitive to unusually high or low temperatures at the breeding grounds than recently arrived migrants (Sol et al. 2005); male Asian Short-toed Larks would therefore be expected to be more easily affected by higher than average spring temperatures. The synchrony of the timing of peak T plasma concentrations between species in 2015 may reflect the lower spring temperature recorded in that year.

Estradiol stimulates sexual behavior in female birds via the central neural system (Eising et al. 2001; Eda-Fujiwara et al. 2003; Hunt and Wingfield 2004; Adkinsregan 2008; Aurélie et al. 2010; Christensen et al. 2012). Our results show that plasma E_2 in both species peaked at the same time, suggesting that both migrant and resident females can start breeding simultaneously.

Changes of thyroid hormone

T_3 can promote the synthesis of DNA, RNA, cellular proteins and increase metabolic rates (Peng et al. 2010; Vézina et al. 2011; Welcker et al. 2013; Zhang et al. 2013). Plasma T_3 levels of seasonally breeding birds increase during the pre-breeding period in preparation for higher energy consumption during breeding (Smith 1982; Pathak and Chandola 1983). Our results show that the plasma T_3 concentrations in both species increased in early spring and peaked simultaneously in both 2014 and

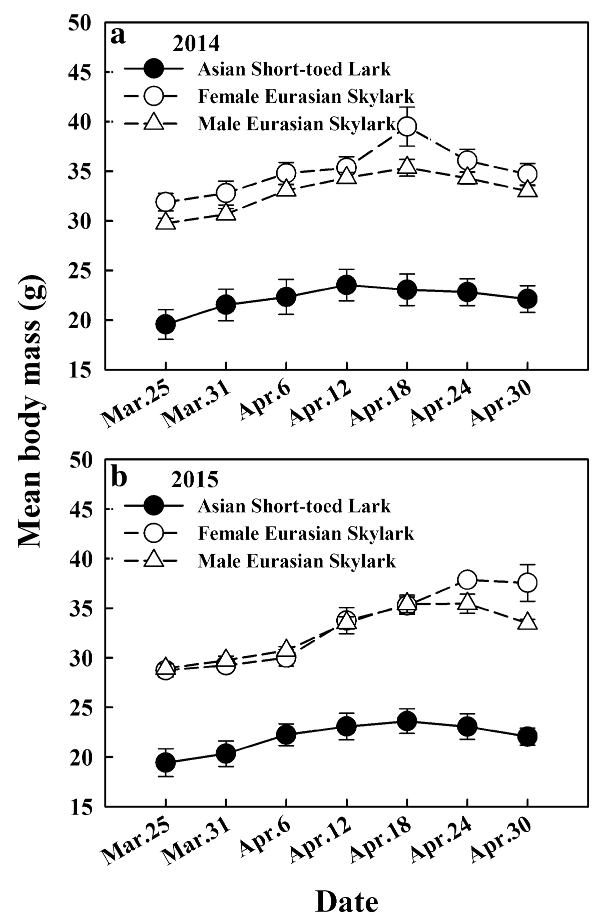

Fig. 6 Temporal trends in body mass in wild Asian Short-toed Larks and Eurasian Skylarks. All the Asian Short-toed Larks and Eurasian Skylarks had been captured in the wild and sampled while held in captivity in 2014 (**a**) and 2015 (**b**)

2015, suggesting that migratory birds can increase their metabolic rate at the same time as resident birds. In addition, our results also show that plasma T_3 levels peaked earlier in both species than plasma LH. Reproduction requires elevated energy consumption (Jorg et al. 2014), therefore increasing the metabolic rate is essential preparation for reproduction. From this perspective, plasma T_3 concentrations should rise earlier than LH concentrations. The differences in the concentrations of T_3 on the same sample date between the two species should be explained as the species specific features.

Changes of body mass

Breeding is so energetically demanding that many bird species have a negative energy balance while breeding, necessitating the accumulation of energy reserves before breeding commences (Zina and Salvante 2010). Body mass is a comprehensive index that reflects the balance of energy intake, energy expenditure and nutritional status (McNab 2009). The body mass of birds often increases with increasing food abundance in spring (Both and Visser 2005; Cooper 2007; Fischer et al. 2010) and females with higher body mass can lay eggs earlier (Neto and Gosler 2010). Our results show that Asian Short-toed Lark attained its maximum body mass earlier than the Eurasian Skylark in both 2014 and 2015, suggesting that resident species accumulate energy reserves faster than migrants. There could be two explanations for this. The first is because the digestive organs of migratory birds, such as the intestines, liver and pancreas, atrophy in order to minimize body weight and facilitate flight; these organs take time to regain normal size and function after arrival at the breeding grounds (McWilliams and Karasov 2001). Secondly, in addition to accumulating fat, migratory species also need to recover muscle protein consumed during migration but the rate of protein accumulation is slower than that of fat (McWilliams and Karasov 2001).

Differences between years

Finally, the difference in the dates when each species attained peak body mass in 2014 and 2015 maybe due to the higher spring temperature in 2014 (Fig. 1). Our results suggest that both the migratory Eurasian Skylark and the resident Short-toed Lark can advance their physiological preparation for breeding in response to warmer spring temperatures. Temperature-controlled experiments are, however, required to confirm this hypothesis.

Conclusion

Migratory Eurasian Skylarks were able to increase their levels of reproductive and thyroid hormones at the same time as resident Asian Short-toed Larks, but the latter were able to increase their body mass faster. Although the Eurasian Skylarks needed more time to regain their body condition, migration did not otherwise appear to delay their physiological preparation for reproduction. The rate of T secretion in Asian Short-toed Larks had been accelerated by the higher spring temperature recorded in 2014, which suggests that resident species might adapt to current climate change more quickly than the migrant species.

Authors' contributions

SZ conceived of the study and designed the experiments. LZ, XX, LG, WW and WL conducted the experiments. LZ wrote the first draft of the article. SZ supervised the research and revised the draft. All authors read and approved the final manuscript.

Author details

[1] College of Life and Environment Sciences, Minzu University of China, Beijing 100081, China. [2] Ministry of Education Key Laboratory for Tropical Animal and Plant Ecology, College of Life Sciences, Hainan Normal University, Haikou 571158, China.

Acknowledgements
This research was supported by grants from the National Nature Science Foundation of China (No. 31372225), the Minzu University Research fund (ydzxxk201619, ydzxxk201618) and 111 Project (B08044).

Competing interests
The authors declare that they have no competing interests.

Availability of data and materials
The datasets generated during and/or analyzed during the current study are available from the corresponding author on a reasonable request.

Ethics approval and consent to participate
Our experimental procedures complied with the current laws on animal welfare and research in China and had the approval of the Animal Research Ethics Committee of Hainan Normal University. In addition, all procedures followed standard protocols, such as the ARRIVE guidelines for reporting animal research.

Received: 16 November 2016 Accepted: 20 March 2017
Published online: 05 April 2017

References
Adkinsregan E. Do hormonal control systems produce evolutionary inertia? Phil Trans R Soc B. 2008;363:1599–609.
Aurélie G, Frédéric A, Clément CC, Colette T, Børge M, Claus B, Geir WG, Olivier C. Stress and the timing of breeding: glucocorticoid-luteinizing hormones relationships in an arctic seabird. Gen Comp Endocr. 2010;169:108–16.
Both C, Visser ME. The effect of climate change on correlation between avian life-history traits. Glob Change Biol. 2005;11:1606–13.
Carey C. Female reproductive energetics. In: Carey C, editor. Avian energetics and nutritional ecology. New York: Chapman & Hall; 1996. p. 324–74.
Chastel O, Lacroix A, Kersten M. Pre-breeding energy requirements: thyroid hormone, metabolism and the timing of reproduction in house sparrows *Passer domesticus*. J Avian Biol. 2003;34:298–306.
Chastel O, Lacroix A, Weimerskirch H, Gabrielsen GW. Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. Horm Behav. 2005;47:459–66.
Christensen A, Bentley GE, Cabrera R, Ortega HH, Perfito N, Wu TJ, Micevych P. Hormonal regulation of female reproduction. Horm Metab Res. 2012;44:587–91.
Cooper SJ. Daily and seasonal variation in body mass and visible fat in mountain chickadees and juniper titmice. Wilson J Ornithol. 2007;119:720–4.
Davies S, Behbahaninia H, Giraudeau M, Meddle SL, Waites K, Deviche P. Advanced seasonal reproductive development in a male urban bird is reflected in earlier plasma luteinizing hormone rise but not energetic status. Gen Comp Endocr. 2015;181:1–10.
Dawson A, King VM, Bentley GE, Ball GF. Photoperiodic control of seasonality in birds. J Biol Rhythm. 2001;16:365–80.
Dawson A. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. Phil Trans R Soc B. 2008;363:1621–33.
Dominoni DM, Hof TJV, Partecke J. Social cues are unlikely to be the single cause for early reproduction in urban European blackbirds (*Turdus merula*). Physiol Behav. 2015;142:14–9.
Eda-Fujiwara H, Suzuki M, Kimura T. Behavioral responses of males to estradiol-treated females in the budgerigar (*Melopsittacus undulatus*). J Ethol. 2003;21:23–8.
Eising CM, Eikenaar C, Schwabl H, Groothuis TGG. Maternal androgens in black-headed gull (*Larus ridibundus*) eggs: consequences for chick development. Proc R Soc Lond B. 2001;268:839–46.
Fischer B, Dieckmann U, Taborsky B. When to store energy in a stochastic environment. Evolution. 2010;65:1221–32.
Garamszegi LZ, Hirschenhauser K, Bokony V, Eens M, Hurtrez-Bousses S, Møller AP, Oliveira RF, Wingfield JC. Latitudinal distribution, migration, and testosterone levels in birds. Am Nat. 2008;172:533–46.
Greives TJ, Fudickar AM, Atwell JW, Meddle SL, Ketterson ED. Early spring sex differences in luteinizing hormone response to gonadotropin releasing hormone in co-occurring resident and migrant dark-eyed juncos (*Junco hyemalis*). Gen Comp Endocr. 2016;236:17–23.
Griffiths R, Daan S, Dijkstra C. Sex identification in birds using two CHD genes. Proc R Soc Lond B. 1996;263:1251–6.
Hegemann A, Matson KD, Versteegh MA, Tieleman BI. Wild Skylark seasonally modulate energy budgets but maintain energetically costly inflammatory immune responses throughout the annual cycle. PLoS ONE. 2012;7:e36358.
Hunt KE, Wingfield JC. Effect of estradiol implants on reproductive behavior of female Lapland longspurs (*Calcarius lapponicus*). Gen Comp Endocr. 2004;137:248–62.
Jenni L, Jenni-Eiermann S, Spina F, Schwabl H. Regulation of protein breakdown and adrenocortical response to stress in birds during migratory flight. Am J Physiol Regul Integr Comp Physiol. 2000;278:1182–9.
Jodie MJ, Joel WM, Joseph MC, Timothy JG, Eric AS, George EB, Ellen DK. Testosterone response to GnRH in a female songbird varies with stage of reproduction: implications for adult behaviour and maternal effects. Funct Ecol. 2007;21:767–75.
Jorg W, Speakman JR, Elliott KH, Hatch SA, Kitaysky AS. Resting and daily energy expenditures during reproduction are adjusted in opposite directions in free-living birds. Funct Ecol. 2014;29:250–8.
Li M, Yin YJ, Hie CY, Qu LN, Zhang GF, Liang YT, Zhao XJ, Liu JS. Seasonal variations of plasma thyroid hormone and its effect on thermoregulation in tree sparrow (*Passer montanus*). Sichuan J Zool. 2010;29:530–4.
Lou LX. Preliminary observation of Eurasian Skylark breeding behaviors. Chin J Zool. 1966;1:19–22.
McGlothlin JW, Ketterson ED. Hormone-mediated suites as adaptations and evolutionary constraints. Phil Trans R Soc B. 2008;363:1611–20.
McNab BK. Ecological factors affect the level and scaling of avian BMR. Comp Biochem Physiol A. 2009;152:22–45.
McWilliams SR, Karasov WH. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. Comp Biochem Physiol A. 2001;128:579–93.
Morbey YE, Ydenberg C. Protandrous arrival to breeding areas: a review. Ecol Lett. 2001;4:663–73.
Neto JM, Gosler AG. Variation in body condition of breeding Savi's Warblers *Locustella luscinioides*: the reproductive stress and flight adaptation hypothesis revisited. J Ornithol. 2010;151:201–10.
Nilsson JA, Raberg L. The resting metabolic cost of egg laying and nestling feeding in great tits. Oecologia. 2001;128:187–92.
Pathak VK, Chandola A. Seasonal variations in circulating thyroxine and triiodothyronine concentrations in spotted munia *Lonchura punctulata*. Gen Comp Endocr. 1983;50:201–4.
Peng LJ, Tang XL, Liu JS, Meng HT. The effect of thyroid hormone on basal thermogenesis (*Pycnonotus sinensis*). Acta Ecol Sin. 2010;30:1500–7.
Ricklefs RE. Energetics of reproduction in birds. In: Paynter RA, editor. Avian energetics. Cambridge: Chapman & Hall; 1974. p. 152–292.
Silverin B, Wingfield J, Stokkan KA, Massa R, Järvinen A, Andersson NA, Lambrechts M, Sorace A, Blomqvist D. Ambient temperature effects on photo induced gonadal cycles and hormonal secretion patterns in Great Tits from three different breeding latitudes. Horm Behav. 2008;54:60–8.
Smith JP. Changes in blood levels of thyroid hormones in two species of passerine birds. Condor. 1982;84:160–70.
Sol D, Lefebvre L, Rodriguez-Teijeiro JD. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Phil Trans R Soc B. 2005;272:1433–41.
Stevenson IR, Bryant DM. Climate change and constraints on breeding. Nature. 2000;406:366–7.
Tian S, Wang WW, Zhang SP, Dou HS, Wu MR, Liu ST. The breeding ecology of *Calandrella cheleensis* in Dalai Lake National Nature Reserve of Inner Mongolia. Sichuan J Zool. 2015;34:453–7.
Tonra CM, Marra PP, Holberton RL. Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. J Avian Biol. 2011;42:397–404.
Vézina F, Dekinga A, Piersma T. Shorebirds' seasonal adjustments in thermogenic capacity are reflected by changes in body mass: how preprogrammed and instantaneous acclimation work together. Integr Comp Biol. 2011;51:394–408.

Wang AZ, Lei FM. Periodical variations of weight and fat reserves in *Onychostruthus taczanowskii*. Sichuan J Zool. 2011;30:560–3.
Washburn BE, Millspaugh JJ, Morris DL, Schulz JH, Faaborg J. Using a commercially available enzyme immunoassay to quantify testosterone in avian plasma. Condor. 2007;109:181–6.
Welcker J, Chastel O, Gabrielsen GW, Guillaumin J, Kitaysky AS, Speakman JR, Tremblay Y, Bech C. Thyroid hormones correlate with basal metabolic rate but not field metabolic rate in a wild bird species. PLoS ONE. 2013;8:e56229.
Wingfield JC, Lynn S, Soma K. Avoiding the "costs" of testosterone: ecological bases of hormone-behavior interactions. Brain Behav Evol. 2001;57:239–51.
Yasuo S, Yoshimura T. Comparative analysis of the molecular basis of photoperiodic signal transduction in vertebrates. Integr Comp Biol. 2009;49:507–18.
Yen PM. Physiological and molecular basis of thyroid hormone action. Physiol Rev. 2001;81:1097–142.
Zhang Y, Yao X, Song YY, Ying H. Thyroid hormone and metabolic regulation. Chin Bull Life Sci. 2013;25:176–83.
Zhao LD, Wang RM, Wu YN, Wu MS, Zhang WH, Liu JS. Daily variation in body mass and thermoregulation in male Hwamei (*Garrulax canorus*) at different seasons. Avian Res. 2015;6:4.
Zheng WH, Lin L, Liu JS, Xu XJ, Li M. Geographic variation in basal thermogenesis in little buntings: relationship to cellular thermogenesis and thyroid hormone concentrations. Comp Biochem Physiol A. 2013;164:483–90.
Zina FV, Salvante KG. Behavioral and physiological flexibility are used by birds to manage energy and support investment in the early stages of reproduction. Curr Zool. 2010;56:767–92.