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Time trees and clock genes: a systematic review and comparative analysis of contemporary avian migration genetics

Louis-Stéphane Le Clercq[1,2,*], Gaia Bazzi[3], Jacopo G. Cecere[3], Luca Gianfranceschi[4], Johannes Paul Grobler[2], Antoinette Kotzé[1,2], Diego Rubolini[5,6], Miriam Liedvogel[7,8] and Desiré Lee Dalton[9]

[1]*South African National Biodiversity Institute, P.O. Box 754, Pretoria, 0001, South Africa*
[2]*Department of Genetics, University of the Free State, PO Box 339, Bloemfontein, 9300, South Africa*
[3]*Area Avifauna Migratrice, Istituto Superiore per la Protezione e la Ricerca Ambientale, via Ca' Fornacetta 9, Ozzano Emilia (BO), I-40064, Italy*
[4]*Dipartimento di Bioscienze, Università degli Studi di Milano, via Celoria 26, Milan, I-20133, Italy*
[5]*Dipartimento di Scienze e Politiche Ambientali, Università degli Studi di Milano, via Celoria 26, Milan, I-20133, Italy*
[6]*Istituto di Ricerca sulle Acque, IRSA-CNR, Via del Mulino 19, Brugherio (MB), I-20861, Italy*
[7]*Max Planck Research Group Behavioral Genomics, Max Planck Institute for Evolutionary Biology, Plön, 24306, Germany*
[8]*Institute of Avian Research, An der Vogelwarte 21, Wilhelmshaven, 26386, Germany*
[9]*School of Health and Life Sciences, Teesside University, Middlesbrough, TS1 3BA, UK*

ABSTRACT

Timing is a crucial aspect for survival and reproduction in seasonal environments leading to carefully scheduled annual programs of migration in many species. But what are the exact mechanisms through which birds (class: Aves) can keep track of time, anticipate seasonal changes, and adapt their behaviour? One proposed mechanism regulating annual behaviour is the circadian clock, controlled by a highly conserved set of genes, collectively called 'clock genes' which are well established in controlling the daily rhythmicity of physiology and behaviour. Due to diverse migration patterns observed within and among species, in a seemingly endogenously programmed manner, the field of migration genetics has sought and tested several candidate genes within the clock circuitry that may underlie the observed differences in breeding and migration behaviour. Among others, length polymorphisms within genes such as *Clock* and *Adcyap1* have been hypothesised to play a putative role, although association and fitness studies in various species have yielded mixed results. To contextualise the existing body of data, here we conducted a systematic review of all published studies relating polymorphisms in clock genes to seasonality in a phylogenetically and taxonomically informed manner. This was complemented by a standardised comparative re-analysis of candidate gene polymorphisms of 76 bird species, of which 58 are migrants and 18 are residents, along with population genetics analyses for 40 species with available allele data. We tested genetic diversity estimates, used Mantel tests for spatial genetic analyses, and evaluated relationships between candidate gene allele length and population averages for geographic range (breeding- and non-breeding latitude), migration distance, timing of migration, taxonomic relationships, and divergence times. Our combined analysis provided evidence (*i*) of a putative association between *Clock* gene variation and autumn migration as well as a putative association between *Adcyap1* gene variation and spring migration in migratory species; (*ii*) that these candidate genes are not diagnostic markers to distinguish migratory from sedentary birds; and (*iii*) of correlated variability in both genes with divergence time, potentially reflecting ancestrally inherited genotypes rather than contemporary changes driven by selection. These findings highlight a tentative association between these candidate genes and migration attributes as well as genetic constraints on evolutionary adaptation.

* Author for correspondence (Tel.: +2782 551 5895; E-mail: leclercq.l.s@gmail.com).
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I. INTRODUCTION

Each year, billions of birds take to the sky to make their annual journey from non-breeding to breeding grounds, often migrating at night with several key stop-over sites to refuel and rest along well-established flyways. This event occurs like clockwork, carefully timed to ensure an optimal flight to reach their destination. These annual flight plans are orchestrated to balance day length (Sockman & Hurlbert, 2020), night-time visibility (Brown & Mewaldt, 1968; Pyle *et al.*, 1993; Norevik *et al.*, 2019), and time spent at staging sites (Roques *et al.*, 2022). The repeated occurrence of this characteristic behaviour on an annual basis with seemingly little deviation has sparked interest in the field of chronobiology, with

emphasis on both intrinsic as well as environmental cues contributing to timekeeping in birds (Åkesson *et al.*, 2017).

To maintain their schedules, annual life events such as moult, fattening, migratory behaviour, and breeding are tied to many extrinsic or environmental factors (*Zeitgebers*) including changes in photoperiod (length of sunlight; Leclerc *et al.*, 2010), changing temperatures (Jenni & Kéry, 2003; Pancerasa *et al.*, 2018), and availability of food sources (Hau & Gwinner, 1996; Stephan, 2002; Scheuerlein & Gwinner, 2002). For many migratory bird species, however, it has been demonstrated that they persistently exhibit seasonally appropriate migration-related behaviours, such as migratory restlessness (*Zugunruhe*) and moulting phenology, even when kept under constant conditions in captivity (Newton, 2007; Aguilar-Roblero, Díaz-Muñoz & Fanjul-Moles, 2015). Therefore, a possible intrinsic mechanism of timekeeping may exist that can function in isolation from environmental factors and may be under genetic control, although involvement of an epigenetic effect has also been proposed (Saino *et al.*, 2017; Merlin & Liedvogel, 2019).

One mechanism of intrinsic annual timekeeping is the circadian clock, which regulates daily activity in almost every organism from bacteria to mammals (Aguilar-Roblero, 2015). The circadian clock comprises several genes which can be defined as: '… genes that interact with each other to make up an auto-regulatory feedback loop, in which its activation and repression cycle takes about one day' (Albrecht & Ripperger, 2009, p. 759). Circadian clock genes therefore have a central axis with a positive feedback loop, which promotes transcription, and a negative feedback loop, which prevents transcription (Fig. 1), and the expression levels of these key elements fluctuate throughout the day in different tissues (Albrecht & Ripperger, 2009; Aguilar-Roblero, 2015) in response to signal transduction of light exposure. For example, as the photoperiod changes due to the orbit of the Earth and seasonality, with days becoming shorter/longer and nights becoming longer/shorter (see Figs 2 and 3), the internal phase of the circadian clock adjusts in order to maintain appropriate sleep–wake cycles in a process known as entrainment (Albrecht & Ripperger, 2009; Robart, McGuire & Watts, 2018). Previous observations of length polymorphisms within these genes in several model species (Tauber & Kyriacou, 2005; O'Malley & Banks, 2008) have found evidence of selection for specific variants along a latitudinal gradient. As photoperiod is tied to latitude, this partially explains how environmental changes modulate the circadian clock on a circannual basis possibly driving the timing and duration of migration (see Fig. 3).

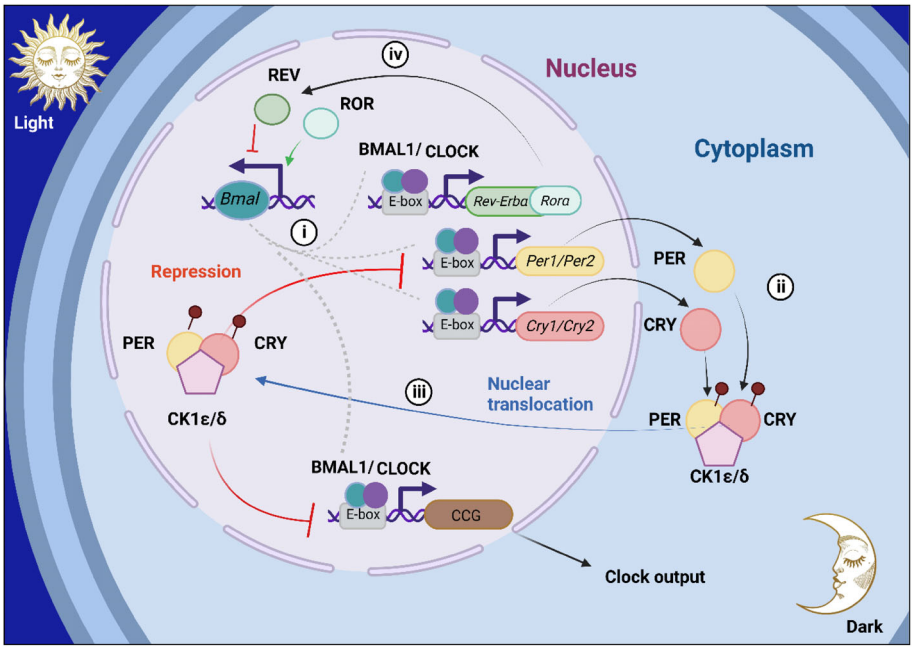

Fig. 1. Diagrammatic representation of the regulation of the circadian clock. (i) Brain and muscle ARNT-like protein 1 (BMAL1, blue circles) forms a dimer with circadian locomotor output cycles protein kaput (CLOCK, purple circles) in the nucleus, which binds to the enhancer box (E-box, grey) region of nuclear receptors (*Rev-Erbα*, green) and retinoic acid-related orphan nuclear receptors (*Rorα*), as well as the *Period 1* or *2* (Per1/2, yellow), *Cryptochrome 1* or *2* (Cry1/2, orange), and other circadian clock genes (CCGs, brown). (ii) When the dimer binds to the *Per1/Per2* and *Cry1/Cry2* E-box, PER and CRY proteins are expressed and, following phosphorylation, form a complex with casein kinase 1 isoform epsilon or delta (CK1ε/δ) in the cytoplasm. (iii) The PER/CRY/CK1ε/δ complex then undergoes nuclear translocation (blue arrow) where it downregulates *Per1/Per2*, *Cry1/Cry2*, and other CCG transcription by inhibiting the binding of BMAL1/CLOCK complexes to E-box regions (red lines). (iv) Concurrently, the binding of BMAL1/CLOCK complexes to the enhancer elements of *Rev-Erbα* and *Rorα* results in the expression of the REV and ROR proteins which act on the transcription elements of *Bmal1*, with REV acting as an inhibitor and ROR acting as an inducer. (Created with BioRender.com).

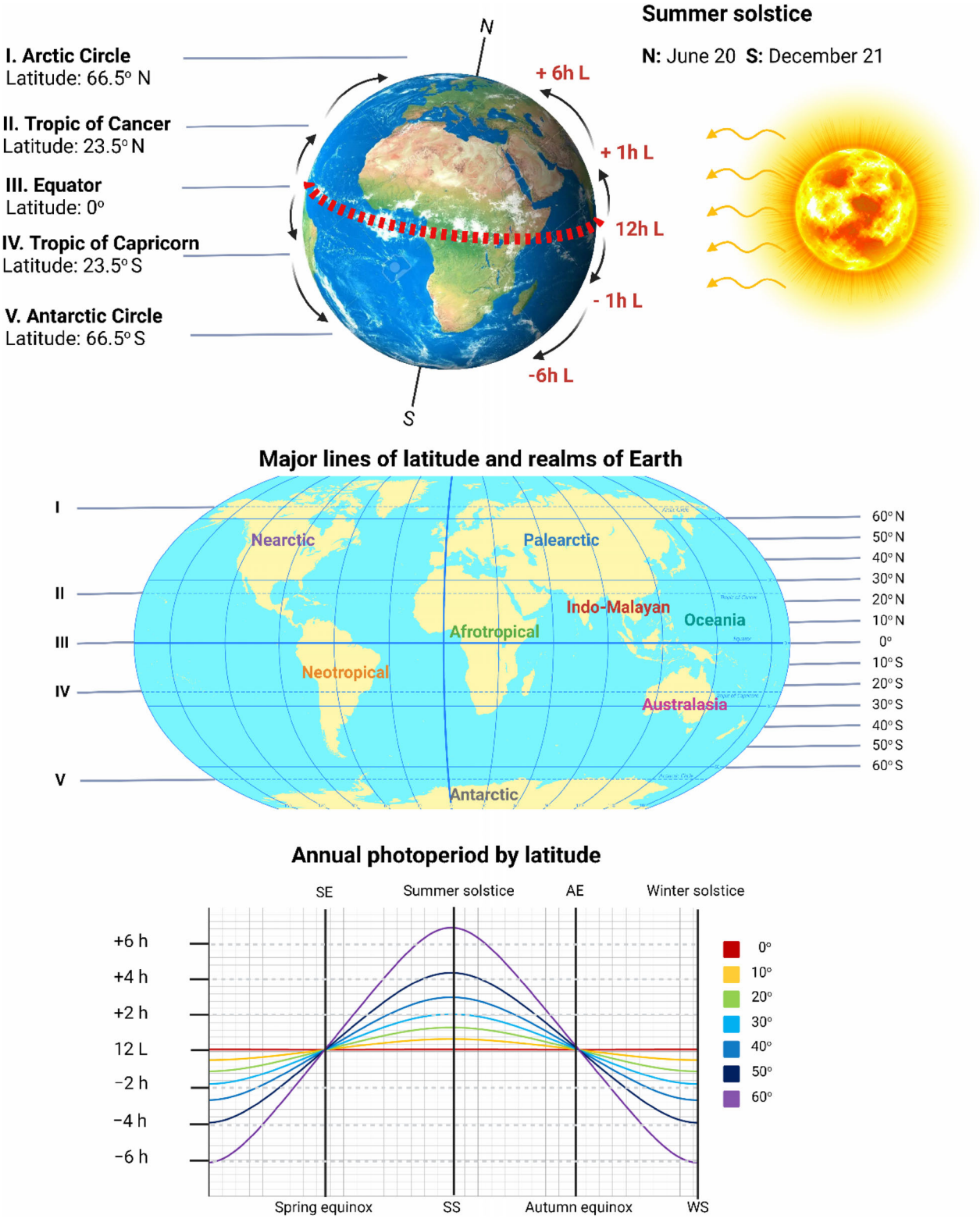

Fig. 2. Diagrammatic representation of the major lines of latitude of Earth and the relative photoperiod at each latitude between the four key dates for changing photoperiods. In the top panel, the orientation of the Earth at the summer solstice is indicated with the difference in day length between the equator (broken line) and the two major tropics and the polar circles. In the centre panel, these lines are indicated on a map, along with the intermediate lines of latitude. In the bottom panel, the annual variation in photoperiod is plotted for each 10° increment in latitude across the year. (Created with BioRender.com).

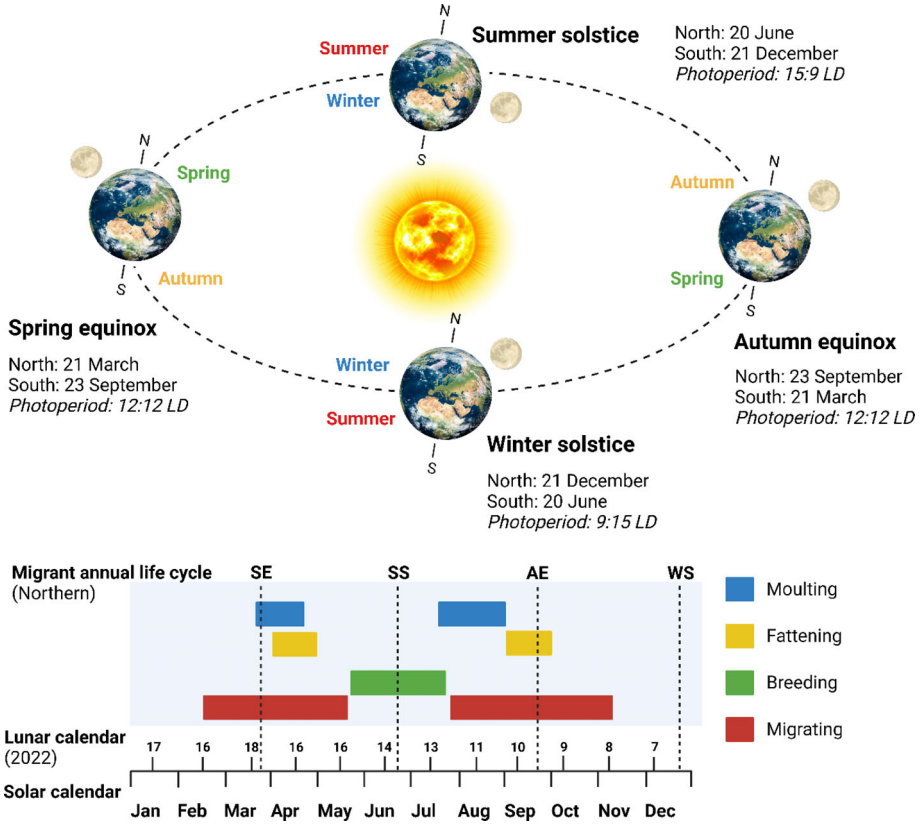

Fig. 3. Diagrammatic illustration of the seasonal cycles of the year indicating the four key dates for changing photoperiods of the year: the summer solstice, the winter solstice, the spring equinox, and the autumn equinox. The equinoxes correspond to near-equal day and night [12 h light:12 h dark; (12:12 LD)] while the summer solstice is the longest day (15:9 LD) and the winter solstice is the shortest day (9:15 LD). The dates of the solstices and equinoxes fall on the exact opposite days in the northern and southern hemispheres each year. The bottom panel indicates the annual timing of major life events during the year for migrants of the northern hemisphere, which encompasses most migratory species in this review. Dates are adapted from the literature and are shown relative to the solar and lunar calendars. (Created with BioRender.com).

One confounding observation for the argument that migration and annual life events are genetically programmed, with birds of the same species expected to have similar genotypes and therefore similar migration strategies resulting from these genotypes, is the occurrence of differential migration patterns within a single species. Differential migration describes the observation that specific populations or groups within a single species follow divergent migratory strategies. These patterns of differential migration include differences in the timing, direction, duration, or distance of migration as well as the occurrence of migration behaviour itself: many birds do not exhibit migratory behaviour but instead form resident populations within their range (Spina & Volponi, 2008, 2009; Billerman *et al.*, 2022). The current view regarding resident populations of bird species is that their ancestors were migratory and that subpopulations adapted to be resident on an individual basis (de Zoeten & Pulido, 2020).

For example, species such as the streaky-breasted flufftail, *Sarothrura boehmi* (Reichenow) (Taylor & Kirwan, 2020), and European bee-eater, *Merops apiaster* (Linnaeus) (Fry & Boesman, 2020), show distinct subpopulations of resident and migratory birds. Migration studies on congeneric spotted eagle hybrids between *Clanga clanga* (Pallas) and *Clanga pomarine* (Brehm) have shown that hybridisation between species with divergent movement patterns has resulted in a new population with migration strategies that differ from their progenitors (Väli *et al.*, 2018). Scandinavian populations of the common chaffinch, *Fringilla coelebs* (Linnaeus) were originally described by Linnaeus as a 'bachelor bird' (Linnaeus, 1758) due to the earlier timing and longer migration of females whereas males appeared nearly resident year-round. By contrast, in most species the males are often the first to depart or migrate further (Dierschke, Mendel & Schmaljohann, 2005; Briedis *et al.*, 2019). This raises the question as to how differential responses to environmental stimuli, and resulting variable migration patterns, are established and maintained between individuals within a species or between closely related subspecies if migration behaviour is a genetically programmed trait.

Several approaches have identified putative polymorphic repeats within clock-regulating genes for use in behaviour

Table 1. Summary of candidate gene studies relating polymorphisms in clock genes to migration-related behaviour. Studies are grouped based on the groupings of species used in Section III. The number of known subspecies (Ssp.) is indicated along with the total alleles and most frequent allele, the Poly-Q allele for *Clock* and *NPAS*, the fragment length for *Adcyap1* and *CREB1*, and the presence of a single nucleotide polymorphism (SNP) for *DRD4*. Studies used latitude/longitude/spatial analyses (a), migratory restlessness (b), timing of egg laying/breeding (c), clutch size (d), timing of migration (e), moult rate (f), urbanisation (g) or exploratory behaviour (h). Symbols against species names indicate migration status: M, migrant; PM, partial migrant; S, sedentary. Species with an asterisk were part of a cross-species shared flyway study that did not include species-level analyses.

Species	Ssp.	Reference	*Clock*	*Adcyap1*	*CREB1*	*NPAS*	*DRD4*	Study method
1(a) Tits:								
Blue tit (*Cyanistes caeruleus*)^{PM}	9	Johnsen *et al.* (2007)	9 (Q_{12})					a
Blue tit (*Cyanistes caeruleus*)^{PM}	9	Liedvogel *et al.* (2009, 2012)	6 (Q_{12})					a, c, d
Blue tit (*Cyanistes caeruleus*)^{PM}	9	Steinmeyer *et al.* (2009)	5 (Q_{12})	7 (162)	7 (548)	5 (Q_{12})		–
Great tit (*Parus major*)^{PM}	15	Liedvogel & Sheldon (2010)	5 (Q_{14})					c
Great tit (*Parus major*)^{PM}	15	Korsten *et al.* (2010)					SNP	h
Great tit (*Parus major*)^{PM}	15	Mueller *et al.* (2013*a*)					SNP	h
1(b) Warblers:								
Blackpoll warbler (*Setophaga striata*)^{M}	1	Ralston *et al.* (2019)	4 (Q_{6})	16 (189)				a, e
Common whitethroat (*Curruca communis*)*,^{M}	4	Bazzi *et al.* (2016*a*)	9 (Q_{10})	13 (172)				a, e
Eastern subalpine warbler (*Curruca cantillans*)*,^{M}	2	Bazzi *et al.* (2016*a*)	4 (Q_{9})	7 (168)				a, e
Eurasian blackcap (*Sylvia atricapilla*)^{PM}	5	Mueller *et al.* (2011)	8 (Q_{8})	13 (161)	10 (532)	2 (Q_{8})	SNP	a, b
Eurasian blackcap (*Sylvia atricapilla*)^{PM}	5	Mettler *et al.* (2015)		11 (161)				e
Eurasian reed warbler (*Acrocephalus scirpaceus*)*,^{M}	4	Bazzi *et al.* (2016*a*)	1 (Q_{11})	10 (169)				a, e
Garden warbler (*Sylvia borin*)*,^{M}	2	Bazzi *et al.* (2016*a*)	6 (Q_{11})	6 (169)				a, e
Great reed warbler (*Acrocephalus arundinaceus*)*,^{M}	2	Bazzi *et al.* (2016*a*)	2 (Q_{12})	2 (163)				a, e
Icterine warbler (*Hippolais icterina*)*,^{M}	1	Bazzi *et al.* (2016*a*)	2 (Q_{8})	7 (169)				a, e
Sedge warbler (*Acrocephalus schoenobaenus*)*,^{M}	1	Bazzi *et al.* (2016*a*)	1 (Q_{11})	5 (163)				a, e
Seychelles warbler (*Acrocephalus sechellensis*)^{PM}	1	Edwards *et al.* (2015)					SNP	h
Willow warbler (*Phylloscopus trochilus*)*,^{M}	3	Bazzi *et al.* (2016*a*)	5 (Q_{9})	10 (174)				a, e
Willow warbler (*Phylloscopus trochilus*)^{M}	3	Bazzi *et al.* (2017)	5 (Q_{9})	10 (174)	4 (529)	5 (Q_{10})		e, f
Wilson's warbler (*Cardellina pusilla*)^{M}	3	Bazzi *et al.* (2016*b*)	2 (Q_{9})	9 (158)				a, e
Wood warbler (*Phylloscopus sibilatrix*)*,^{M}	1	Bazzi *et al.* (2016*a*)	3 (Q_{11})	5 (162)				a, e
1(c) Swallows:								
Barn swallow (*Hirundo rustica*)^{M}	7	Dor *et al.* (2011)	3 (Q_{7})					a, c
Barn swallow (*Hirundo rustica*)^{M}	7	Caprioli *et al.* (2012)	3 (Q_{7})					c
Barn swallow (*Hirundo rustica*)^{M}	7	Bazzi *et al.* (2015)	3 (Q_{7})					e
Chilean swallow (*Tachycineta meyeni*)^{M}	1	Dor *et al.* (2012)	3 (Q_{8})					a, c, d
Mangrove swallow (*Tachycineta albilinea*)^{S}	1	Dor *et al.* (2012)	2 (Q_{8})					a, c, d
Tree swallow (*Tachycineta bicolor*)^{M}	1	Dor *et al.* (2012)	4 (Q_{8})					a, c, d
Tree swallow (*Tachycineta bicolor*)^{M}	1	Bourret & Garant (2015)	4 (Q_{8})	13 (173)	3 (518)	7 (Q_{11})		a, c
Violet-green swallow (*Tachycineta thalassina*)^{M}	2	Dor *et al.* (2012)	4 (Q_{8})					a, c, d

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Table 1. *(Cont.)*

Species	Ssp.	Reference	*Clock*	*Adcyap1*	*CREB1*	*NPAS*	*DRD4*	Study method
White-rumped swallow (*Tachycineta leucorrhoa*)[M]	1	Dor *et al.* (2012)	3 (Q_7)					a, c, d
1(d) Larks:								
Asian short-toed lark (*Alaudala cheleensis*)[PM]	4	Zhang *et al.* (2017)	6 (Q_9)					c
1(e) Sparrows, juncos, and buntings:								
Dark-eyed junco (*Junco hyemalis*)[PM]	14	Peterson *et al.* (2013)	7 (Q_{11})	16 (161)				a, b
Yellow-eyed junco (*Junco phaeonotus*)[S]	4	Peterson *et al.* (2013)	5 (Q_{11})	11 (161)				a, b
Song sparrow (*Melospiza melodia*)[M]	25	Posliff (2020)					SNP	a, h
1(f) Cardinals:								
Painted bunting (*Passerina ciris*) [M]	2	Contina *et al.* (2018)	6 (Q_{11})	4 (169)				e
1(g) Flycatchers and chats:								
African stonechat (*Saxicola torquatus*)[S]	16	Justen *et al.* (2022)	6 (Q_{13})					a, e
Bluethroat (*Cyanecula svecica*)[M]	12	Johnsen *et al.* (2007)	7 (Q_{13})					a
Canary island stonechat (*Saxicola dacotiae*)[S]	1	Justen *et al.* (2022)	3 (Q_{14})					a, e
Collared flycatcher (*Ficedula albicollis*)[M]	1	Krist *et al.* (2021)	4 (Q_{12})	6 (182)	9 (534)	4 (Q_{11})		e
Common nightingale (*Luscinia megarhynchos*)[M]	3	Saino *et al.* (2015*a*)	5 (Q_{12})	7 (151)				e
Common nightingale (*Luscinia megarhynchos*)*,[M]	3	Bazzi *et al.* (2016*a*)	5 (Q_{12})	7 (151)				a, e
Common redstart (*Phoenicurus phoenicurus*)*,[M]	2	Bazzi *et al.* (2016*a*)	4 (Q_{14})	13 (169)				a, e
European pied flycatcher (*Ficedula hypoleuca*)[M]	3	Kuhn *et al.* (2013)	5 (Q_{12})					a, c
European pied flycatcher (*Ficedula hypoleuca*)[M]	3	Saino *et al.* (2015*a*)	5 (Q_{12})	11 (180)				e
European pied flycatcher (*Ficedula hypoleuca*)*,[M]	3	Bazzi *et al.* (2016*a*)	5 (Q_{12})	11 (180)				a, e
European stonechat (*Saxicola rubicola*)[M]	2	Justen *et al.* (2022)	7 (Q_{14})					a, e
Northern wheatear (*Oenanthe oenanthe*)*,[M]	4	Bazzi *et al.* (2016*a*)	5 (Q_{14})	6 (167)				a, e
Siberian stonechat (*Saxicola maurus*)[M]	5	Justen *et al.* (2022)	5 (Q_{13})					a, e
Spotted flycatcher (*Muscicapa striata*)*,[M]	7	Bazzi *et al.* (2016*a*)	2 (Q_9)	5 (162)				a, e
Whinchat (*Saxicola rubetra*)[M]	1	Saino *et al.* (2015*a*)	7 (Q_{14})	13 (169)				e
Whinchat (*Saxicola rubetra*)*,[M]	1	Bazzi *et al.* (2016*a*)	7 (Q_{14})	13 (169)				a, e
1(h) Pipits:								
Tree pipit (*Anthus trivialis*)[M]	2	Saino *et al.* (2015*a*)	5 (Q_9)	12 (170)				e
Tree pipit (*Anthus trivialis*)*,[M]	2	Bazzi *et al.* (2016*a*)	5 (Q_9)	12 (170)				a, e
1(i) Thrushes:								
Eurasian blackbird (*Turdus merula*)[PM]	7	Mueller *et al.* (2013*b*)	2 (Q_7)	20 (165)	2 (532)	3 (Q_{10})	SNP	g
Mountain bluebird (*Sialia currucoides*)[M]	1	Sauve *et al.* (2021)		7 (169)			SNP	a
Western bluebird (*Sialia mexicana*)[PM]	6	Sauve *et al.* (2021)		7 (170)			SNP	a
1(j) Shrikes and orioles:								
Eurasian golden oriole (*Oriolus oriolus*)*,[M]	1	Bazzi *et al.* (2016*a*)	2 (Q_6)	7 (163)				a, e
Woodchat shrike (*Lanius senator*)*,[M]	3	Bazzi *et al.* (2016*a*)	3 (Q_6)	8 (176)				a, e
2(a) Buzzards, hawks, and kites:								
Eurasian buzzard (*Buteo buteo*)[S]	6	Chakarov *et al.* (2013)	1 (Q_8)	3 (152)	3 (533)	2 (Q_9)		a, c, e
Northern goshawk (*Accipiter gentilis*)[S]	10	Chakarov *et al.* (2013)	2 (Q_{11})		1 (534)	2 (Q_{11})		a, c, e

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Table 1. *(Cont.)*

Species	Ssp.	Reference	*Clock*	*Adcyap1*	*CREB1*	*NPAS*	*DRD4*	Study method
Red kite (*Milvus milvus*)^{S}	2	Chakarov *et al.* (2013)	2 (Q_8)	2 (139)	2 (534)	2 (Q_8)		a, c, e
2(b) Hoopoes:								
Eurasian hoopoe (*Upupa epops*)*,^{M}	7	Bazzi *et al.* (2016*a*)	3 (Q_8)	3 (157)				a, e
2(c) Wrynecks:								
Eurasian wryneck (*Jynx torquilla*)*,^{M}	6	Bazzi *et al.* (2016*a*)	4 (Q_8)	5 (135)				a, e
2(d) Bee-eaters:								
European bee-eater (*Merops apiaster*)*,^{M}	1	Bazzi *et al.* (2016*a*)	1 (Q_4)	6 (163)				a, e
2(e) Nightjars:								
European nightjar (*Caprimulgus europaeus*)*,^{M}	6	Bazzi *et al.* (2016*a*)	2 (Q_8)	7 (154)				a, e
2(f) Doves:								
European turtle dove (*Streptopelia turtur*)*,^{M}	4	Bazzi *et al.* (2016*a*)	2 (Q_7)	5 (150)				a, e
2(g) Shorebirds:								
Bar-tailed godwit (*Limosa lapponica baueri*)^{M}	6	Parody-Merino *et al.* (2019)	6 (Q_9)					a, e
Collared plover (*Charadrius collaris*)^{S}	1	de Almeida Miranda *et al.* (2022)		6 (172)				a
Semipalmated plover (*Charadrius semipalmatus*)^{M}	1	de Almeida Miranda *et al.* (2022)		5 (178)				a
Semipalmated sandpiper (*Calidris pusilla*)^{M}	1	de Almeida Miranda *et al.* (2022)		6 (188)				a
Spotted sandpiper (*Actitis macularius*)^{M}	1	de Almeida Miranda *et al.* (2022)		4 (196)				a
Yellow-legged gull (*Larus michahellis*)^{PM}	2	Romano *et al.* (2018)	2 (Q_5)	4 (162)		1 (Q_7)		b, c
Other:								
Black swan (Anseriformes: Anatidae, *Cygnus atratus*)^{S}	1	Van Dongen *et al.* (2015)					SNP	g, h

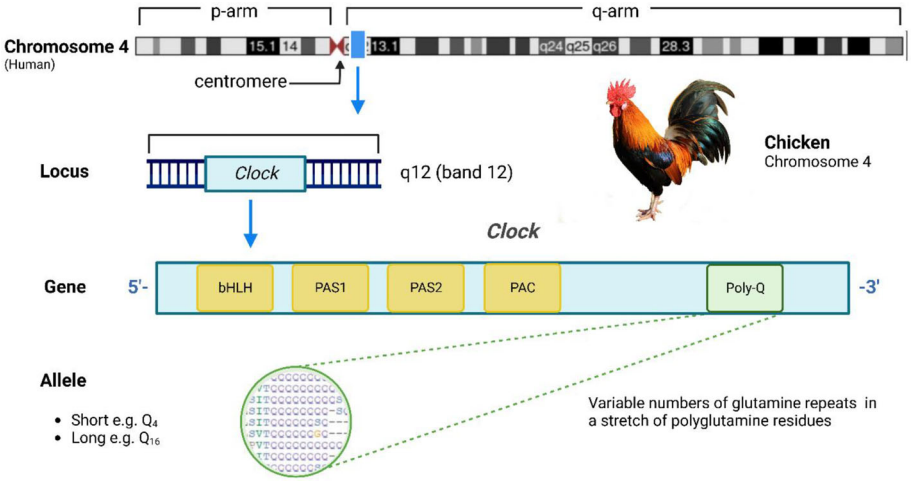


Fig. 4. Depiction of the *Clock* gene (NCBI Gene ID: 9575) and its variable polyglutamine (Poly-Q) repeat region associated with migration phenology. At the top of the figure, the location of *Clock* in the human genome on chromosome 4 at position 12.0 on the q-arm is shown. Below is the gene transcript with its four primary domains in yellow: basic helix–loop–helix (bHLH), period-ah receptor nuclear translocator (ARNT)–single minded protein (PAS1/PAS2), and PAS-associated C-terminal (PAC). The Poly-Q region is indicated in green; this is a region of glutamine (Q) residues that varies in length within and among species. (Created with BioRender.com).

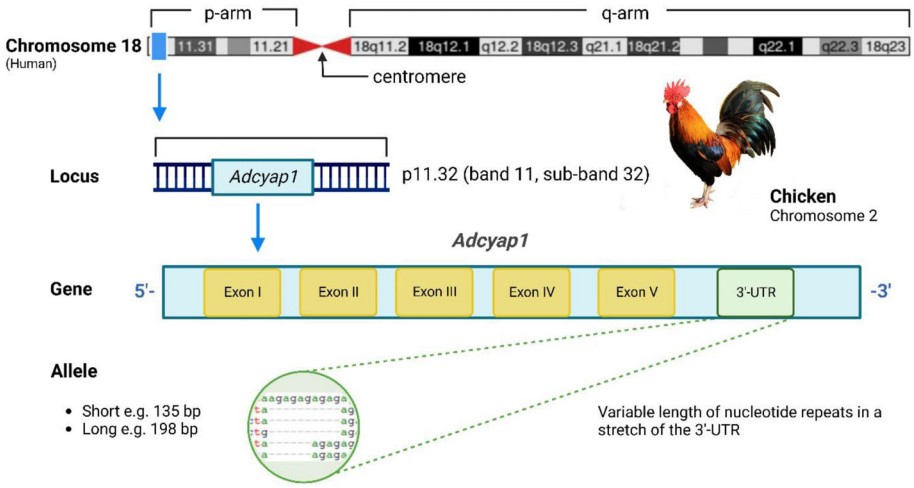


Fig. 5. Depiction of the *Adcyap1* gene (NCBI Gene ID: 116) and its variable 3′-untranslated region (UTR) associated with migration phenology. At the top of the figure, the location of *Adcyap1* in the human genome on chromosome 18 at position 11.32 on the p-arm of the chromosome is shown. Below this is the gene transcript with the five exons indicated in orange. The 3′-UTR is indicated in green; this region contains a stretch of nucleic acid repeats of adenine and guanine that vary in number within and among species. (Created with BioRender.com).

association studies of birds (Steinmeyer, Mueller & Kempenaers, 2009). Steinmeyer *et al.* (2009) described polymorphic genes in the blue tit [recently separated into the Eurasian blue tit, *Cyanistes caeruleus* (Linnaeus), and African blue tit, *Cyanistes teneriffae* (Lesson)]. They also developed methods to assay the identified polymorphisms in Eurasian blackcap *Sylvia atricapilla* (Linnaeus) populations. Several candidate genes (summarised in Table 1) have since been tested, including *Clock*, *Adcyap1*, *CREB1*, *NPAS2*, and *DRD4*. Of these genes, *Clock* and *Adcyap1* have been studied most extensively.

The *Clock* gene (Fig. 4) is located on chromosome 4 at the 12th band of the q-arm in humans and on chromosome 4 in chickens, *Gallus domesticus* (Linnaeus). Towards the 3′-end there is a polyglutamine repeat (Poly-Q) region that can vary in length among and within species, resulting in shorter and longer alleles. For this gene, changes in entrainment resulting from length polymorphisms have been hypothesised to result from changes in protein folding and binding entropies but this has not yet been confirmed (Johnsen *et al.*, 2007). A second gene, *Adcyap1* (Fig. 5), encodes the pituitary-adenylate cyclase-activating polypeptide (PACAP) protein which stimulates the production of melatonin in the pineal gland, thereby conveying light information from the retina to the brain and regulating the circadian rhythm (Simonneaux, Ouichou & Pévet, 1993; Hannibal *et al.*, 1998). *Adcyap1* is located on chromosome 18 of the human genome, at band 11.32 of the p-arm and on chromosome 2 in chickens. The 3′-untranslated region (3′-UTR) contains a homopolymer run of adenine (A) and guanine (G) which can vary in length within and among species, resulting in shorter and longer alleles. For this gene the putative differences in entrainment could be related to altered post-transcriptional regulation of its messenger RNA (mRNA), due to increased instability or metabolic changes (Puga *et al.*, 2005; Steri *et al.*, 2018).

Studies have investigated questions surrounding differential migratory behaviour by comparing migratory attributes (or related breeding phenology) of individuals or populations to putative variation within candidate clock genes (Caprioli *et al.*, 2012; Saino *et al.*, 2015*a*; Delmore *et al.*, 2016). The central hypothesis in these candidate gene studies, including those on birds (Johnsen *et al.*, 2007; Steinmeyer *et al.*, 2009) is that variation, in the form of length polymorphisms within genes associated with the circadian clock, may result in differential responses to environmental cues due to delayed or enhanced entrainment, resulting in differences in migration behaviour which may drive speciation through a migratory divide that establishes selection for specific genotypes based on the photoperiod/latitude of breeding and non-breeding ranges.

A significant association between candidate gene variability and factors contributing to migration patterns, annual synchronicity in life events, or geographical processes has been illustrated in multiple species-specific studies across several lineages within the order Passeriformes, including Palaearctic and Nearctic warblers (Bazzi *et al.*, 2017; Ralston *et al.*, 2019), swallows (Caprioli *et al.*, 2012; Bazzi *et al.*, 2015), tits (Liedvogel *et al.*, 2009), chats (Justen *et al.*, 2022), and flycatchers (Kuhn *et al.*, 2013); whilst associations were not clear or absent for other lineages (Contina *et al.*, 2018; Parody-Merino *et al.*, 2019). Additionally, although some heritability was observed in a study comparing migratory species from several lineages that share the same trans-Saharan migratory flyway (Bazzi *et al.*, 2016*a*), a cross-species comparative study on a subset of candidate genes failed to detect a clear, generalised relationship between clock gene diversity and divergence between migratory *versus* resident bird species (Lugo Ramos, Delmore & Liedvogel, 2017). This defies the expectation that genes that strongly influence and are selected for

in shaping migratory behaviour will be conserved among species that exhibit similar migratory behaviour, although other factors such as size differences (Mettler, Segelbacher & Schaefer, 2015), diet (Stephan, 2002), and habitat preference (Väli *et al.*, 2018) may alter the degree of influence of genetic effects that use only the photoperiod as a *zeitgeber*.

Furthermore, these studies often only considered contemporary ranges and did not consider the role of palaeogeography in shaping ranges throughout the evolutionary history of these species (Meert, 2012; Voelker, Bowie & Klicka, 2013). This is critical for two reasons: firstly, selection is postulated to be stronger during speciation events at the time of divergence and diminish over time (Nosil, Harmon & Seehausen, 2009), and secondly, only parts of the geographic regions within their range represent likely historical ranges before speciation while others represent more recent colonisation events after speciation (Olson *et al.*, 2001; Le *et al.*, 2022). This includes periods where currently separated continents would have been connected, such as Laurasia, the supercontinent that included parts of Africa, North America, and Eurasia, as well as periods of high fragmentation such as the sea formerly separating Europe and Asia as well as the North American inland sea (Western interior seaway) that separated the western and eastern parts of modern North America (Kauffman, 1984). A further case exists for the colonisation of islands including insular India (Prasad & Parmar, 2022), after it separated from Madagascar but before it merged with Asia, as well as islands that formed more recently such as the Cape Verde islands that formed ∼40–50 million years ago (MYA) while the Canary islands formed ∼20 MYA (Schmincke, 1976).

Thus, the current literature on the putative role of these polymorphisms in shaping differential migration among bird species provides conflicting evidence that needs to be clarified to reframe our understanding of migration genetics. Furthermore, the context within which the data are interpreted may need reappraisal due to frequent taxonomic revisions that occur in bird classification and disparities that exist between phylogeny and taxonomy for species concepts (Sangster, 2014), particularly if closely related taxa inherited a specific subset of genotypes that potentially restrict plasticity in future behavioural adaptation and therefore fitness. This is of particular importance as understanding how a biological clock is able to anticipate environmental cues and adapt to them, along with any potential genetic constraints, is of relevance to conservation given the potential effects of climate change and habitat erosion on migratory behaviour (Carey, 2009).

The aim of this review is to (*i*) systematically synthesise and review the existing literature on polymorphisms in clock genes, primarily within the context of migration, breeding, and annual life events, to identify existing patterns, (*ii*) perform a comparative analysis of the existing data to test for an association between shared clock gene polymorphisms and similarities in attributes of migration such as latitude, distance, and timing, and (*iii*) contextualise the resulting evidence in a taxonomically, phylogenetically, and palaeogeographically informed manner to compare similarities within and among lineages with shared evolutionary histories.

II. METHODS

(1) Literature search and systematic review

A systematic approach was used to search for and synthesise the available literature. Literature was searched on the *Scopus* (www.scopus.com) and *Dimensions* (www.dimensions.ai) databases using the following Boolean search string: ('Clock genes' OR 'Clock' OR 'Adcyap1') AND ('Birds' OR 'Avian') AND ('Migration' OR 'Flying'). Search results were exported in the comma separated value format and the literature was subsequently summarised, guided by citation networks visualised using *CitNetExplorer* 1.0.0 and *VOSviewer* 1.6.16 (van Eck & Waltman, 2017). The results retrieved from *Scopus* were converted into the appropriate format using the R package *Scopus2CitNet* 0.1.0.0 in *RStudio* 1.4.1106 (RStudio Team, 2021), running R version 4.0.5 (R Core Team, 2020). Due to the diverse array of species in which these studies were conducted, the literature was organised by year of publication followed by species, with taxonomic grouping based firstly on order (passerine or non-passerine), followed by family. Families were grouped, based on higher taxonomic classifications, into superfamilies and parvorders for the sake of a concise and cohesive comparison (see Section III); warblers, which is a paraphyletic group, are discussed together as they share significant overlaps in morphology.

(2) Species

Species for comparative analysis were selected based on the existing literature for either the *Clock* or *Adcyap1* gene in relation to migration phenology and/or for which genomic or transcriptomic studies have been conducted. This included unpublished data from eight species: American redstart, *Setophaga ruticilla* (Linnaeus); common chiffchaff, *Phylloscopus collybita* (Vieillot); common yellowthroat, *Geothlypis trichas* (Linnaeus); hermit thrush, *Catharus guttatus* (Pallas), magnolia warbler, *Setophaga magnolia* (Wilson); Swainson's thrush, *Catharus ustulatus* (Nuttall), and white-throated sparrow, *Zonotrichia albicollis* (Gmelin). As most studies thus far have focused on Palearctic and Nearctic birds, species were further complemented with data (see Section II.3) for migrant and resident bird species from other locations to have a globally distributed data set. This included the addition of several species of manakins, resident birds found in equatorial regions of the Neotropics, the endangered Elfin woods warbler, *Setophaga angelae* (Kepler & Parkes), endemic to Puerto Rico, and the Australasian superb fairy-wren, *Malurus cyaneus* (Ellis). Our final species list included 76 species (76 for *Clock* and 71 for *Adcyap1*) of which 58 were classified as migrants and 18 were classified as residents. Migrants were defined

as species with complete or partial migratory behaviour (i.e. species with both resident and migratory populations); species with a single resident population that was not sampled were treated as migratory. Residents were defined as species that do not follow an annual cycle of migration (although they may follow a pattern of altitudinal migration within their resident range); species with a single migratory population that was not sampled were treated as resident.

Inclusion in subsequent analyses was based on data availability in two categories: (*i*) the availability of genetic data as either within-population-level data on individual alleles for *Clock* or *Adcyap1* or records of the most common allele for the species from the literature or online databases, as well as species availability for the phylogenetic tree from the Bird Tree website (see Section II.3); (*ii*) the availability of migration data including migration dates for each migratory season as well as shapefile data for GIS to compute different parameters related to migration (see Section II.4). As far as possible, species were only included if they share one of the major migratory flyways with more than one other included species and therefore experience similar *Zeitgebers* for annual synchronicity.

(3) Genetic data

Population-level allele data were retrieved for 40 species (39 for *Clock* and 37 for *Adcyap1*) from either the supplementary material of the article or the online data repositories *Dryad* (www.datadryad.org), *Figshare* (www.figshare.com), or directly from the article authors (see Section VII, Acknowledgements). *Clock* data were transformed to represent the actual number of poly-Q repeats, as different studies used different primers resulting in variable lengths in the raw data. *Adcyap1* was consistently amplified and sequenced using the same primer set or region, facilitating between study comparisons. Sequence data were not available for all species, so the total reported allele length of *Adcyap1* was used rather than the length of the AG-repeat region alone. However, this will not alter our central hypothesis that any length difference could result in altered gene regulation resulting in different migration-related traits.

Data summarised from the literature included species, number of alleles, most common allele, and observed heterozygosity when available. Additional information such as the number of extant and presently recognised subspecies was retrieved from *Birds of the World* (Billerman *et al.*, 2020). *Clock* and *Adcyap1* data for additional species (see Section II.2), from a wider geographic distribution and including additional resident birds, was retrieved from the National Centre for Biotechnology Information (NCBI) website using Basic Local Alignment and Search Tool (BLAST) searches (Altschul *et al.*, 1990) against reference genomes and available databases, including *PopSet* and *Nucleotide* (Agarwala *et al.*, 2018); where no sequence data were available a further BLAST search was carried out against the Sequence Read Archive (SRA) for specific species. The tree used for the phylogeny was generated from the 'Ericson' phylogeny (Jetz *et al.*, 2012) by sampling 5000 trees from the Bird Tree website (www.birdtree.org) for available species from the list of 76. The trees were summarised to a 60% consensus tree by maximum clade credibility using *TreeAnnotator* 2.6.3, part of BEAST 2.6.3 (Bouckaert *et al.*, 2014), with a 10% burn-in.

(4) Migration and range data estimates

Migration data were computed using *QGIS* 3.16.15 (QGIS Development Team, 2022) from shapefiles extracted from the geodatabase of distribution maps compiled by BirdLife International, version 2021.1 (BirdLife International & Handbook of the Birds of the World, 2021), supplemented with shapefile data from eBird (Fink *et al.*, 2021). Centroids were computed for the non-breeding and breeding ranges to determine the average coordinates by latitude and longitude (in degrees) for each. The average migration distance between these centroids was calculated (in metres). Geographic distance matrices for the breeding and non-breeding coordinates of each species were generated with the java application *Geographic Distance Matrix Generator* 1.2.3 (Ersts, 2012) in degrees. Species classified as partial migrants, for which breeding and non-breeding range data were available, were treated as migrants, while data-deficient partial migrants were treated as resident birds. For resident species, the calculations were based on their full range.

When population and species-specific migration dates were not stated in the source publications, this information was retrieved from eBird (Fink *et al.*, 2021) or, for species sampled in Italy, from the Italian bird migration atlas (Spina & Volponi, 2008, 2009) or, for Asian buntings and larks, from Ali, Ripley & Roberts (1999). As seasons and migration dates vary according to hemisphere, dates were normalised to a standard reference point (Sockman & Hurlbert, 2020) that roughly corresponds to the photoperiod and temperature (see Figs 2 and 3). The difference in days was calculated between the start, middle and end dates for spring migration and the summer solstice [approximately 15 h light:9 h dark (15:9 LD)] and spring equinox (12:12 LD), while autumn migration dates were normalised with reference to the winter solstice (∼9:15 LD) and autumn equinox (12:12 LD), for each respective hemisphere depending on the species range.

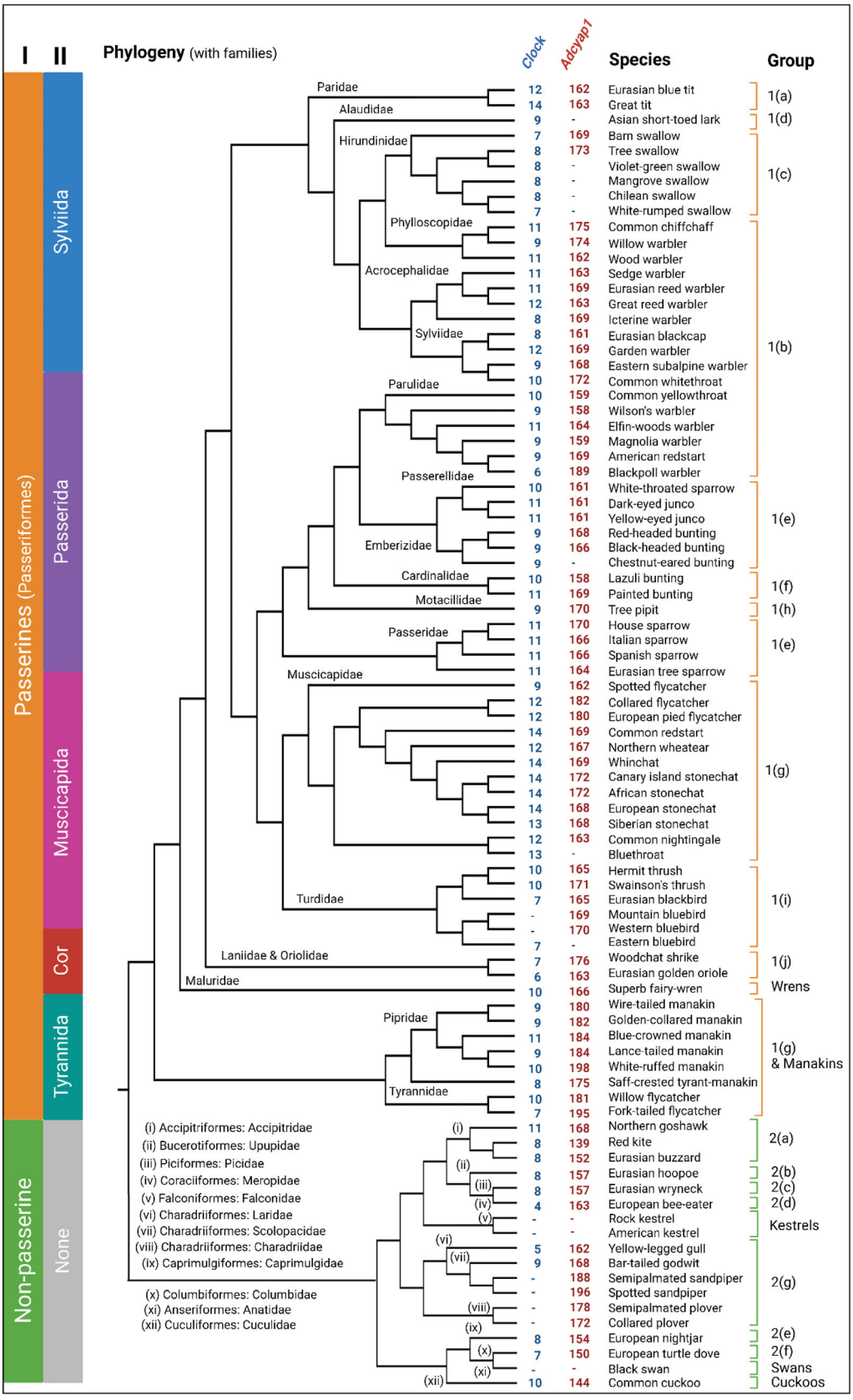
(5) Population genetics

Population genetics analyses were done for the 40 species for which individual allele data was available. POPGENE 1.32 (Yeh *et al.*, 1997) was used to test for Hardy–Weinberg (Hardy, 1908; Weinberg, 1908) equilibrium using chi-squared (χ^2) tests (with significance measured at $\alpha = 0.02$), to calculate the observed (H_o) and expected (H_e) heterozygosity, and to create a genetic distance matrix using fixation index (F_{ST}) values. Python for Population Genetics (*PyPop*) version 0.7.0 (Lancaster *et al.*, 2007) was used to test for selection and neutrality as well as linkage disequilibrium. Neutrality was assessed using Slatkin's implementation

Table 2. Summary of studies that used non-candidate gene approaches to identify genetic regions in birds that either co-vary with migration phenology or are expressed differentially on a circannual basis. Ssp. lists the number of known subspecies. Study methods were transcriptomics (a), genomics (b), or epigenetics (c). Letters against species names indicate migration status: M, migrant; PM, partial migrant; S, sedentary.

Species	Ssp.	Reference	Study method
1(a) Tits:			
Great tit (*Parus major*)^{PM}	15	Laine *et al.* (2019)	a
Great tit (*Parus major*)^{PM}	15	Mäkinen *et al.* (2019)	c
Great tit (*Parus major*)^{PM}	15	Viitaniemi *et al.* (2019)	c
1(b) Warblers:			
Eurasian blackcap (*Sylvia atricapilla*)^{PM}	5	Delmore *et al.* (2020*a*,*b*)	b
Willow warbler (*Phylloscopus trochilus*)^{M}	3	Lundberg *et al.* (2013, 2017)	a, b
Willow warbler (*Phylloscopus trochilus*)^{M}	3	Boss *et al.* (2015)	a
Wilson's warbler (*Cardellina pusilla*)^{M}	3	Ruegg *et al.* (2014*b*)	b
1(c) Swallows:			
Barn swallow (*Hirundo rustica*)^{M}	7	Saino *et al.* (2017)	c
Tree swallows (*Tachycineta bicolor*)^{M}	1	Brown (2019)	a
1(e) Sparrows, juncos, and buntings:			
Black-headed bunting (*Emberiza melanocephala*)^{M}	1	Singh *et al.* (2015)	a
Black-headed bunting (*Emberiza melanocephala*)^{M}	1	Mishra *et al.* (2017)	a
Black-headed bunting (*Emberiza melanocephala*)^{M}	1	Sharma *et al.* (2018*a*)	a
House sparrow (*Passer domesticus*)^{PM}	14	Guldvog (2015)	a
Italian sparrow (*Passer italiae*)^{S}	1	Guldvog (2015)	a
Red-headed bunting (*Emberiza bruniceps*)^{M}	1	Singh *et al.* (2013)	a
Red-headed bunting (*Emberiza bruniceps*)^{M}	1	Sharma *et al.* (2018*b*)	a, c
Red-headed bunting (*Emberiza bruniceps*)^{M}	1	Trivedi *et al.* (2019)	a
Spanish sparrow (*Passer hispaniolensis*)^{PM}	2	Guldvog (2015)	a
White-crowned sparrow (*Zonotrichia leucophrys*)^{PM}	5	Jones *et al.* (2008*a*,*b*)	a
1(f) Cardinals:			
Painted bunting (*Passerina ciris*)^{M}	2	Contina *et al.* (2019)	b
1(g) Flycatchers and chats:			
Northern wheatear (*Oenanthe oenanthe*)^{M}	4	Frias-Soler *et al.* (2020, 2021)	a
1(i) Thrushes:			
Bicknell's thrush (*Catharus bicknelli*)^{M}	1	Voelker *et al.* (2013)	b
Black-billed nightingale-thrush (*Catharus gracilirostris*)^{S}	2	Voelker *et al.* (2013)	b
Black-headed nightingale-thrush (*Catharus mexicanus*)^{S}	3	Voelker *et al.* (2013)	b
Eurasian blackbird (*Turdus merula*)^{PM}	7	Franchini *et al.* (2017)	a
Gray-cheeked thrush (*Catharus minimus*)^{M}	2	Voelker *et al.* (2013)	b
Hermit thrush (*Catharus guttatus*)^{PM}	9	Voelker *et al.* (2013)	b
Orange-billed nightingale-thrush (*Catharus aurantiirostris*)^{PM}	14	Voelker *et al.* (2013)	b
Ruddy-capped nightingale-thrush (*Catharus frantzii*)^{S}	7	Voelker *et al.* (2013)	b
Russet nightingale-thrush (*Catharus occidentalis*)^{S}	4	Voelker *et al.* (2013)	b
Slaty-backed nightingale-thrush (*Catharus fuscater*)^{S}	7	Voelker *et al.* (2013)	b
Swainson's thrush (*Catharus ustulatus*)^{M}	6	Voelker *et al.* (2013)	b
Swainson's thrush (*Catharus ustulatus*)^{M}	6	Ruegg *et al.* (2014*a*)	b
Swainson's thrush (*Catharus ustulatus*)^{M}	6	Delmore *et al.* (2015, 2016)	b
Swainson's thrush (*Catharus ustulatus*)^{M}	6	Johnston *et al.* (2016)	b
Veery (*Catharus fuscescens*)^{M}	4	Voelker *et al.* (2013)	b
Wood thrush (*Hylocichla mustelina*)^{M}	1	Voelker *et al.* (2013)	b
Yellow-throated nightingale-thrush (*Catharus dryas*)^{S}	2	Voelker *et al.* (2013)	b
Other:			
Passerines			
Chestnut-crowned babbler (Pomatostomidae, *Pomatostomus ruficeps*)^{S}	1	Liebl *et al.* (2021)	c
Gray catbird (Mimidae, *Dumetella carolinensis*)^{M}	1	DeMoranville *et al.* (2019)	a
Non-passerines			
American kestrel (Falconiformes: Falconidae, *Falco sparverius*)^{PM}	17	Bossu *et al.* (2022)	b

(Slatkin, 1994) of the Ewens–Watterson (Ewens, 1972; Watterson, 1977) test, with the probability values expressed as the relative degree at which the observed *F*-value occurs in a sample distribution for a simulation run with 10,000 repeats. Linkage disequilibrium was assessed using two measures: the overall linkage disequilibrium, D' (Hedrick, 1987), and Cramer's V Statistic, W_n (Cramer, 1946). $P < 0.05$ is indicative of significant linkage disequilibrium.



(Figure 6 legend continues on next page.)

(6) Mantel tests

Mantel tests (Mantel, 1967) were conducted on the 40 species for which allele data was available using the *Mantel* 2.1.0 (Carr, 2021) package in Python 3.9 (Python Team, 2021). Tests compared the genetic distance within two candidate genes and attributes of migration including the distance between latitudes of breeding and non-breeding ranges among species, as well as the relationship between the genetic distance and taxonomic distance and divergence times as measures of evolutionary distance, to assess the strength of heritability of genotypes within lineages.

Test were run between the genetic distance matrices, generated with *CONVERT* 1.31, the geographic distance matrices, generated with *Geographic Distance Matrix Generator* 1.2.3 (for both breeding and non-breeding coordinates), the taxonomic distance matrices, generated using the R package *vegan* 2.5-7 (Oksanen *et al.*, 2020), and the divergence times matrix. Divergence times between pairs of species were retrieved from the Time Tree resource (Kumar *et al.*, 2017) website (www.timetree.org) using Python Automated Retrieval of Time Trees (*PAReTT* version 1.0.1) and exported as a vectorised matrix. $P < 0.02$ and $\tilde{Z} > 1.96$ (or < -1.96) is considered significant.

(7) Phylogenetic generalised least squares analysis

Phylogenetic generalised least square (PGLS) models were fitted for the full list of 76 species for which the most common allele and migration data were available. Each test was run independently using the R package *caper* 1.0.1 (Orme *et al.*, 2018) to avoid error from repeat sampling. PGLS was used to relate both *Clock* and *Adcyap1* length to breeding and non-breeding latitude (as distance from the equator in degrees), as well as to total migration distance between regions and to the normalised dates for the beginning, middle, and end of spring and autumn migration, assuming Brownian motion and a lambda (λ) = 1.0. The phylogenetic tree used as input for PGLS was retrieved from the Bird Tree website (www.birdtree.org). The phylogenetic signal for each gene was measured using the R package *phytools* 0.7-90 (Revell, 2012) to compute both lambda and kappa for the gene and tree data and verify the presence of Brownian motion.

(8) Time trees and palaeogeography

Trees were downloaded from Bird Tree website (www.birdtree.org) as described in Section II.3. Time trees were computed from calibrated divergence time estimates using the Time Tree resource (Kumar *et al.*, 2017) to visualise the evolutionary history and relatedness of study species in terms of shared common ancestry and the length of time individual lineages have been evolving independently. The relevant topography of Earth for each time period was reconstructed in *GPlates* 2.3.0 (Müller *et al.*, 2018) with the PALEOMAP paleoAtlas (Scotese, 2016). This was used to visualise relevant barriers to gene flow, and potential differences in selective forces between modern and historical geography for each time period that likely would have contributed to selection and speciation across the genomes of the study species.

III. SYSTEMATIC REVIEW OF PUBLISHED STUDIES

The results of studies assaying candidate gene polymorphisms and comparing them to relevant attributes of seasonal phenology are summarised in Table 1. Non-candidate-gene studies, conducted at the genome, epigenome, or transcriptome level, are summarised in Table 2; such studies have frequently complemented candidate gene studies in terms of species coverage. Because many biological traits among birds are highly heritable within lineages (Silva *et al.*, 2017; Lamichhaney *et al.*, 2018; Cava, Perlut & Travis, 2019), our systematic review is structured according to taxonomic group (Fig. 6). The estimated divergence times of families and species for the most pertinent lineages are illustrated in Fig. 7 with the non-passerine orders as an outgroup. Two studies, included in the following comprehensive review, represented cross-species analyses. Bazzi *et al.* (2016*a*), reported individual species clock genes and diversity measures that are highlighted below, however, this study was a cross-species analysis of 23 species that share a single trans-Saharan migratory flyway and did not provide detailed within-species analyses. Lugo Ramos *et al.* (2017) explored general patterns within clock genes to delineate resident and migratory species. Primary findings from these studies are discussed where applicable below.

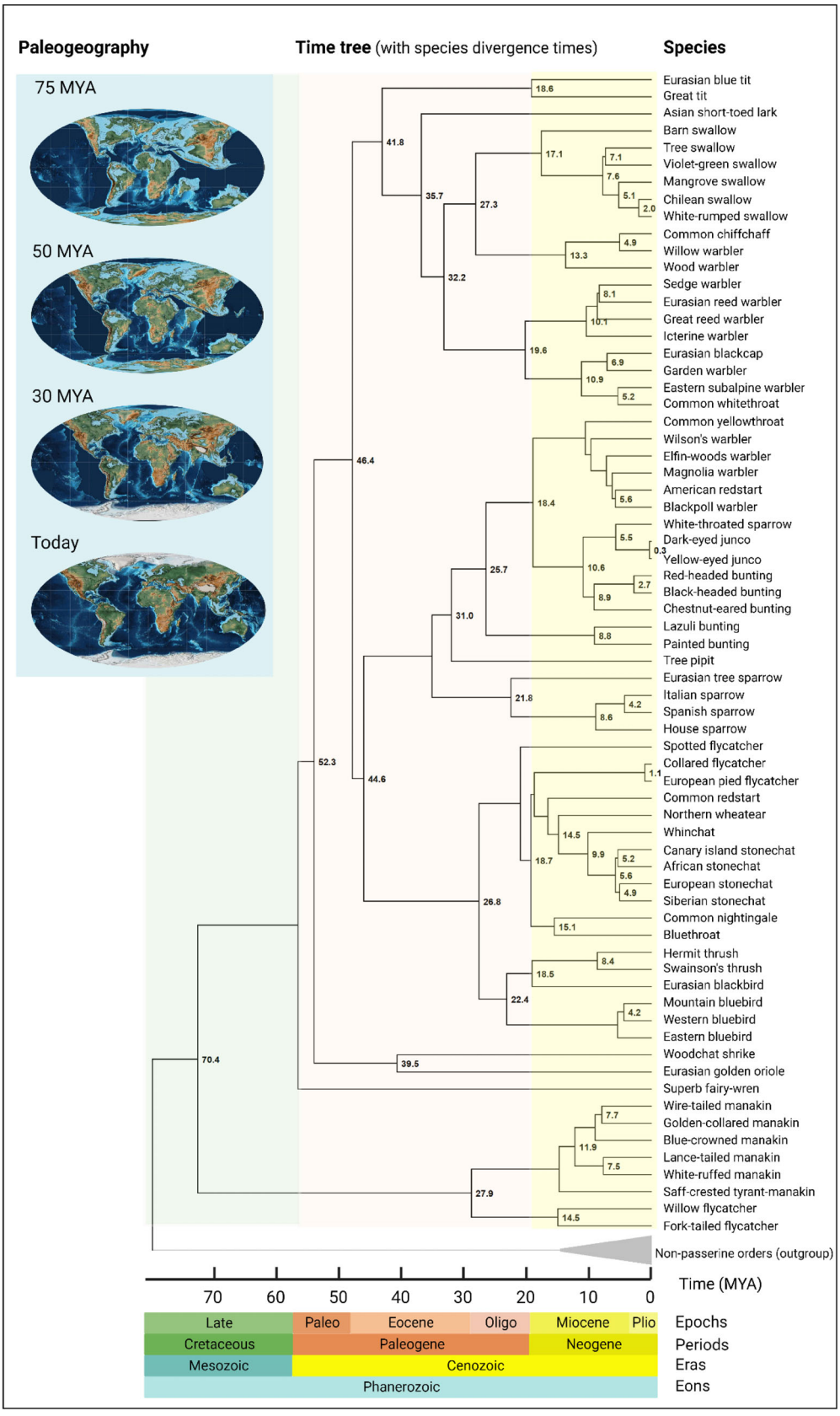
(1) Passerine birds

(*a*) *Tits (Family: Paridae)*

Johnsen *et al.* (2007) were the first to investigate if polymorphic differences in *Clock* exist within avian populations based on evolutionary and functional studies of allelic variants of

(Figure legend continued from previous page.)

Fig. 6. Phylogenetic tree of species in class Aves for which clock genes have been assayed in previous studies, as well as the additional species included in the phylogenetic generalised least squares (PGLS) analysis. This tree was used for both the taxonomic and phylogenetic groupings for comparing studies in the review section, as well as for the input tree used in the PGLS analysis. The tree shows the major taxonomic divisions among species by order (I) and parvorder (II). Families are indicated at the relevant clades of the tree while the main groupings used in Section III are indicated to the right. The most common *Clock* allele (number of Poly-Q repeats) and the length of the most common *Adcyap1* allele (in base pairs) is indicated for each species. Cor, Corvida. (Created with BioRender.com).



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fruit fly (*Drosophila melanogaster*) circadian clock genes (Tauber & Kyriacou, 2005). They characterised *Clock* variation in Poly-Q regions in the context of breeding phenology using 14 blue tit populations, including subspecies, across a latitudinal gradient. They found evidence for significant relationships between latitudinal clines in habitat and *Clock* lengths among 13 of the studied populations, as well as significant levels of allelic differentiation across subspecies. The most common allele was Q_{12} which was found in at least 44% of genotypes, and in all individuals in the Italian subpopulation. They concluded that, at least in the blue tit populations studied, longer *Clock* alleles were correlated with greater clines in habitat, partially distinguished subspecies, and revealed genetic processes not associated with other microsatellite markers (Johnsen *et al.*, 2007). Studies on a single blue tit population in Oxfordshire woods in the UK with records of timing of breeding (Liedvogel *et al.*, 2009) and clutch size (Liedvogel, Cornwallis & Sheldon, 2012) across a two-year period found that shorter *Clock* alleles corresponded to earlier breeding, shortened incubation period, and higher fledging rates among females; allele frequencies were homogenously distributed. This supported the conclusion that *Clock* polymorphisms can be linked to adaptation to local environments, which may explain population variation in this allele in blue tits. Similar phenotypic correlates were not present in the sympatric great tit, *Parus major* (Linnaeus), suggesting that correlations between behaviour and *Clock* polymorphisms may not be universal to all passerines (Liedvogel & Sheldon, 2010), although studies on circadian period length within this species have identified heritable differences in their migratory behaviour (Helm & Visser, 2010).

(*b*) *Warblers (Families: Acrocephalidae, Parulidae, Phylloscopidae, Sylviidae)*

(i) 'Old World warblers'. In the family Sylvidae, *Clock*, *Adcyap1*, *NPAS2*, and *CREB1* were studied in several populations (representing most recognised subspecies) of Eurasian blackcap (Mueller, Pulido & Kempenaers, 2011) including more recent radiations to the Cape Verde islands, in a comparison of length polymorphisms to individual calculated migratory distance. A fifth gene, *DRD4*, which has been linked to 'exploratory behaviour' in great tit populations (Korsten *et al.*, 2010; Mueller *et al.*, 2013*a*) was also analysed. Only *Adcyap1* showed a significant relationship, with longer alleles positively associated with a higher breeding latitude and shorter alleles with a higher degree of migratory restlessness. A study on the Seychelles warbler, *Acrocephalus sechellensis* (Oustalet) (Acrocephalidae) also failed to establish a role for *DRD4* (Edwards *et al.*, 2015).

Bazzi *et al.* (2016*a*) analysed clock genes in common whitethroat, *Curruca* (*Sylvia*) *communis* (Latham), eastern subalpine warbler, *Curruca* (*Sylvia*) *cantillans* (Pallas), and garden warbler, *Sylvia borin* (Boddaert), identifying significant heterozygosity for *Clock* (0.68–0.76) and *Adcyap1* (0.66–0.88).

In the Acrocephalidae, Bazzi *et al.* (2016*a*) studied four species: Eurasian reed warbler, *Acrocephalus scirpaceus* (Hermann), great reed warbler, *Acrocephalus arundinaceus* (Linnaeus), Icterine warbler, *Hippolais icterina* (Vieillot) and sedge warbler, *Acrocephalus schoenobaenus* (Linnaeus). Low diversity was observed within the *Clock* gene in this family with nearly all individuals homozygous for the same allele, while heterozygosity for the *Adcyap1* allele varied from 0.18 to 0.81. Overall, the greatest diversity was observed for great reed warbler which has two known subspecies. No indication was given as to whether sampling included these known subspecies but given the single sampling site on a Mediterranean island it is possible that both subspecies were not included.

In the Phylloscopidae, Bazzi *et al.* (2016*a*) studied two species, willow warbler, *Phylloscopus trochilus* (Linnaeus) and wood warbler, *Phylloscopus sibilatrix* (Bechstein) and found greater *Clock* allele diversity as compared to Acrocephalidae with heterozygosity scores of 0.63 and 0.43 respectively and a similar trend for *Adcyap1*. A later study on willow warbler (Bazzi *et al.*, 2017) identified a high degree of homozygosity for the Q_9 allele, which was present in 98% of all individuals, but no significant relationship was found in relation to migration phenology. *NPAS2* and *CREB1* were also assayed; *NPAS2* positively predicted the date of migration while *CREB1* positively predicted moult speed; both effects were sex-specific and only present in males (Bazzi *et al.*, 2017). In a non-candidate gene approach, mRNA expression levels were measured in willow warblers using transcriptomics to elucidate potential gene candidates (Lundberg *et al.*, 2013; Boss *et al.*, 2015) and whole-genome sequencing (Lundberg *et al.*, 2017). These studies identified distinct haplotype distributions between migratory phenotypes despite low allele variability; with only a fraction of the tested regions showing measurable variations.

(ii) 'New World warblers'. For the Parulidae, data are available for Wilson's warbler, *Cardellina pusilla* (Wilson) (Bazzi *et al.*, 2016*b*) and blackpoll warbler, *Setophaga striata* (Forster) (Ralston *et al.*, 2019). Wilson's warbler showed a high degree

(Figure legend continued from previous page.)

Fig. 7. Time tree of study species indicating the relative divergence times (millions of years ago, MYA), of the major lineages for the species discussed or analysed in this review. The tree was rooted and calibrated with non-passerine orders as an outgroup and therefore reflects below order-level divergence times of the more closely related passerine families, genera, and species. Colour coding is according to the geological periods given below the figure. The inset panel on the top left shows the corresponding palaeogeography from before the continents were fully assembled (75 MYA) to when most continents had assumed their contemporary shape, approximately 30 MYA, and finally assumed their modern-day positions in terms of latitude and longitude (today). (Created with BioRender.com).

of homozygosity for the Q_9 allele and there was no correlation with migration phenology. By contrast, Ralston *et al.* (2019) found a correlation between spring and autumn migration and allele length diversity for both *Clock* and *Adcyap1*.

In a non-candidate gene approach, a panel of single nucleotide polymorphisms (SNPs) in Wilson's warblers was used to assess potential genomic regions driving differences in geographic distribution, with several genomic regions showing evidence for differentiation including many genes related to circadian circuitry (Ruegg *et al.*, 2014*b*).

(c) *Swallows (Family: Hirundinidae)*

Dor *et al.* (2011) analysed the *Clock* Poly-Q region in five populations (including three subspecies) of barn swallow, *Hirundo rustica* (Linnaeus), and found low levels of variability despite evident population structure. Nearly 98% of all allelic diversity was accounted for by the Q_7 allele (Dor *et al.*, 2011). The authors suggested that social cues may take precedence over other environmental cues for migration which could result in negative selection for *Clock* polymorphism. Later studies on European populations of this species revealed a similar pattern, with the Q_7 allele present in 96% of the tested genotypes in Italy (Caprioli *et al.*, 2012) and 91% in Switzerland (Bazzi *et al.*, 2015). Caprioli *et al.* (2012) found an association between *Clock* alleles and breeding phenology in females, while rarer genotypes occurred in males, and Bazzi *et al.* (2015) reported correlations with departure and arrival times. Correlations between genotype and timing of moulting have also been identified (Saino *et al.*, 2013), and annual timing of moulting is known to co-vary with migratory phenology (Saino *et al.*, 2015*b*). The apparently low genetic variability may be due to these genes currently being under directional selection, with this species showing changes in migratory phenology in response to climate change (Altwegg *et al.*, 2012).

Dor *et al.* (2012) studied *Clock* length polymorphisms in five species of *Tachycineta* swallows (Table 1). Tree swallow, *T. bicolor* (Vieillot), violet-green swallow, *T. thalassina* (Swainson) and mangrove swallow, *T. albilinea* (Lawrence) displayed a characteristically higher proportion of the Q_8 allele (64%), whilst white-rumped swallow, *T. leucorrhoa* (Vieillot) had a higher prevalence of the Q_7 allele. Chilean swallow *T. meyeni* (Cabanis) had a near equal distribution of both the Q_7 and Q_8 alleles (Dor *et al.*, 2012). Although the study species came from a wide range of breeding latitudes, no significant correlation was found between breeding latitude and *Clock* mean allele length, although there was a small effect in some species on breeding/laying time in females (Dor *et al.*, 2012). A major limiting factor in this study was that each species was sampled from only one location, meaning that allele diversity and evidence for selection within a species could not be assessed accurately. Bourret & Garant (2015) evaluated polymorphism in four genes in tree swallow in relation to two phenological traits related to migration: laying date and incubation duration. For the *Clock* gene, the Q_8 allele was the most abundant (61.6%). *Adcyap1* was found to be highly polymorphic with 13 alleles (as in Eurasian blackcaps, see Table 1). Significant correlations were observed for all genes measured with environmental variables such as latitude, temperature, and breeding density; in particular, longer alleles were associated with more eastern breeding latitudes (Bourret & Garant, 2015). In a transcriptomics study, several regions were identified that putatively co-varied with migration phenology in tree swallows, although none corresponded to previously identified candidate genes (Brown, 2019).

(d) *Larks (Family: Alaudidae)*

In Asian short-toed lark, *Alaudala* (*Calandrella*) *cheleensis* (Swinhoe), a near-equal distribution of the *Clock* Q_9 and Q_{11} alleles was reported. There was a significant correlation with the timing of egg laying and the seasonal endocrine response that initiates breeding (Zhang *et al.*, 2017). Note that this species is currently under taxonomic review and is not universally recognised as separate from lesser short-toed lark (de Juana & Suárez, 2020; BirdLife International, 2021; HBW and BirdLife International, 2021), although speciation may have occurred during the period that Europe and Asia were separated by a body of water.

(e) *Sparrows, juncos, and buntings (Families: Passerellidae, Emberizidae)*

The Italian sparrow, *Passer italiae* (Vieillot) is a hybrid of the house sparrow *Passer domesticus* (Linnaeus) and Spanish sparrow *Passer hispaniolensis* (Temminck). Despite likely differences in migration behaviour (other closely related sympatric sparrow species are known to show different migratory phenology; Borowske, Gjerdrum & Elphick, 2017), all three species were found to be homozygous for the Q_{11} *Clock* allele (Guldvog, 2015). Higher diversity without evident patterning, but able to partition migrating and sedentary populations, was observed for *Adcyap1*. In white-crowned sparrow, *Zonotrichia leucophrys* (Forster), using transcriptomic approaches (Jones *et al.*, 2008*b*), significant variation was reported in the expression of one clock-related gene, *Copine 4* (*CPNE4*), which has also been observed in other bird species (Ruegg *et al.*, 2014*b*; Delmore *et al.*, 2015; Bossu *et al.*, 2022). A study in song sparrow, *Melospiza melodia* (Wilson), found that exploratory behaviour and migration distance were both correlated with SNPs in *DRD4* among migrants (Posliff, 2020).

A study of 15 populations of the highly divergent junco species complex, including eight subspecies of the dark-eyed junco, *Junco hyemalis* (Linnaeus), and two subspecies of the yellow-eyed junco, *Junco phaeonotus* (Wagler), found no consistent relationship across all congeneric species for *Clock* or *Adcyap1* length polymorphisms and the measured phenological traits. They did, however, find longer *Clock* alleles in two subspecies known to migrate longer distances as well as a relationship between *Adcyap1* length and migratory restlessness in one of two captive populations (Peterson *et al.*, 2013).

Several transcriptomic studies have been carried out on migratory species of the family Emberizidae. Singh, Rani &

Kumar (2013) measured expression levels in captive red-headed bunting, *Emberiza bruniceps* (Brandt), under varying photoperiods, for several genes including *Adcyap1*, *Bmal1*, *Clock*, *Cry1/2*, and *Per2*. A strong correlation between photoperiod and differential gene expression was observed in all the assayed tissue types, providing evidence of light-attuned oscillations within the circadian circuitry of migratory birds (Singh *et al.*, 2013; Leclerc *et al.*, 2010). Higher expression levels were observed under photoperiods consistent with triggers for autumn migration. Spring photoperiods are known to lead to many metabolic and endocrine changes (Sharma *et al.*, 2018*b*). Interestingly, Singh *et al.* (2013) also reported differential expression of the genes for DNA methyltransferase 3 (DNMT3) and Tet methylcytosine dioxygenase 2 (TET2), two enzymes involved in methylation, indicating a possible role for epigenetic control over migratory and non-migratory states as suggested previously for barn swallows (Saino *et al.*, 2017). Transcriptomic studies in the congenic black-headed bunting, *E. melanocephala* (Scopoli), revealed a similar pattern of differential expression in neural and peripheral tissues that oscillated with photoperiod (Singh *et al.*, 2015). These studies did not assess potential inter-individual variation in the measured responses, perhaps because both species of bunting are considered monotypic. These buntings represent species with part of their annual range including India and may represent more recent colonisation of this area after the landmasses merged about 20–40 MYA.

(*f*) *Cardinals (Family: Cardinalidae)*

The painted bunting, *Passerina ciris* (Linnaeus), and the lazuli bunting, *Passerina amoena* (Say), are classified in the family Cardinalidae (Lowther *et al.*, 2020). These species are located on the modern North American continent with early speciation possibly influenced by the presence of the North American interior seaway millions of years ago. Allelic diversity of three painted bunting populations, including both subspecies, was compared for both *Clock* and *Adcyap1*; migration phenology was only analysed in the western population for which geolocator data were available (Contina *et al.*, 2018). Greater allelic diversity was observed for both genes in the western population, with the most common allele Q_{11}; in the eastern population Q_{12} was more abundant. No significant correlation was detected with the initiation or duration of autumn migration, and it was concluded that individual allele studies may have limited resolution for this species. The same authors later assessed differences in migration behaviour between subspecies using a panel of SNPs similar to those used in thrushes (Ruegg *et al.*, 2014*a*) and warblers (Ruegg *et al.*, 2014*b*) and detected at least three distinct breeding populations across the continental USA that may form pertinent conservation units (Contina *et al.*, 2019).

(*g*) *Flycatchers and chats (Family: Muscicapidae)*

Johnsen *et al.* (2007) investigated variation in *Clock* Poly-Q regions in 12 populations of the bluethroat, *Cyanecula* (*Luscinia*) *svecica* (Linnaeus), an Old-World chat. No significant correlation between allelic diversity and latitudinal clines was found, with the Q_{13} allele present in 85.4% of genotypes; all individuals from the Italian subpopulation were homozygous for this allele (Johnsen *et al.*, 2007). A study on the common nightingale, *Luscinia megarhynchos* (Brehm), found a near-equal prevalence of the Q_{11} and Q_{12} alleles with a significant correlation between longer alleles and a later migration date (Saino *et al.*, 2015*a*). In the Northern wheatear, *Oenanthe Oenanthe* (Linnaeus), the most common allele is Q_{14} (Bazzi *et al.*, 2016*a*). Transcriptomic studies on this species detected seasonal differences in the expression of key clock elements in birds with different migration phenologies (Frias-Soler *et al.*, 2020, 2021).

Studies on the European pied flycatcher, *Ficedula hypoleuca* (Pallas), found five *Clock* Poly-Q alleles in contemporary (Saino *et al.*, 2015*a*) and historical samples (Kuhn *et al.*, 2013), with the Q_{12} allele present in 70% of individuals (Saino *et al.*, 2015*a*). Neither study identified a significant association between migration timing and polymorphisms in *Clock* (Kuhn *et al.*, 2013; Saino *et al.*, 2015*a*) or *Adcyap1* (Saino *et al.*, 2015*a*), however, Saino *et al.* (2015*a*) did report a slight relationship between timing and sex. A similar sex-dependent pattern of *Clock* and *Adcyap1* lengths with timing was found in the related spotted flycatcher, *Muscicapa striata* (Pallas) (Bazzi *et al.*, 2016*a*) and whinchat, *Saxicola rubetra* (Linnaeus) (Saino *et al.*, 2015*a*). A recent study in flycatchers evaluated polymorphisms in four *Clock* genes in the collared flycatcher, *Ficedula albicollis* (Temminck), but found no evidence for a relationship between genetic diversity and migration phenology over a four-year period (Krist *et al.*, 2021).

A study on the stonechat species complex (Justen *et al.*, 2022) found no clear correlates between phenological attributes such as breeding latitude and *Clock* genotypes but did detect a relationship with timing of autumn migration for the migratory species. This study included subspecies of the African stonechat, *Saxicola torquatus* (Linnaeus), resident in central Africa but not those of the resident population in South Africa, Canary Island stonechat, *Saxicola dacotiae* (Meade-Waldo), European stonechat, *Saxicola rubicola* (Linnaeus), and Siberian stonechat, *Saxicola maurus* (Pallas), and identified a variety of *Clock* alleles (Q_8–Q_{15}), with the most common alleles being Q_{13} and Q_{14}. The Q_{14} allele similarly was the most common allele observed in the congeneric whinchat (Saino *et al.*, 2015*a*). The Canary island stonechat, which was nearly homozygous for Q_{14}, likely represents a more recent radiation and colonization as the Canary islands were formed approximately 20 MYA.

This illustrates that, at least within the family Muscicapidae, migration phenology may vary independently of genetic polymorphisms but there is evidence for differential expression of circadian clock genes (Frias-Soler *et al.*, 2020).

(*h*) *Pipits (Family: Motacillidae)*

Tree pipits, *Anthus trivialis* (Linnaeus) were found to have relatively short *Clock* alleles (range Q_6–Q_{10}), with the most

prevalent being Q_9 which is found in 85% of the tested genotypes (Saino *et al.*, 2015*a*). Saino *et al.* (2015*a*) reported a significant relationship between migration date and longer alleles in females, but not males. Sex dependence of migration phenology on *Clock* photoperiodic responses remains to be documented for this species. It is possible that such dependence could be related to time of egg laying and hatching, which would be more strongly related to the timing of migration in females as recorded in blue tits (Liedvogel *et al.*, 2009).

(*i*) *Thrushes (Family: Turdidae)*

High-resolution detection of genetic markers was used in the Swainson's thrush, *Catharus ustulatus*, to identify genomic regions related to migration. Several genes were found to have higher levels of differentiation than expected, including genes previously associated with the circadian clock and migratory behaviour such as *Adcyap1*, *CREB1*, *NPAS2*, and *Per3*, between the two subspecies (Ruegg *et al.*, 2014*a*). The authors concluded that future work should include sampling from hybrid zones to assess the potential effect of the observed differentiation on maintaining barriers to gene flow between subspecies (Ruegg *et al.*, 2014*a*). Subsequent studies by Delmore *et al.* (2015) in a hybrid zone between coastal and inland populations of Swainson's thrush used next generation sequencing (NGS) of the whole genome and targeted their analyses to gene regions previously associated with migratory phenology, including *Clock*, *Adcyap1*, *NPAS2* and *DRD4*. Between-group analyses revealed high levels of heterogeneity in diversity estimates, while within-group diversity was lower in areas of higher speciation. Further analyses of the same data set (Delmore *et al.*, 2016) compared known differences in migration phenology and found that three genes co-vary with phenology, one of which was *Clock*. The complex interplay between genes, species concepts, and palaeogeography has also been studied in detail for *Catharus* thrushes (Voelker *et al.*, 2013) using genomic and mitochondrial markers. This study inferred an ancestral range north of Mexico and identified the adaptation of sedentary behaviour within *Catharus* to be correlated with the first speciation events that temporally coincided with range expansion to the newly formed Central America and the closing of the North American inland seaway. This was followed by recolonisation of land connecting the west and east of the continent in the late Pleistocene.

Genetic analysis of clock genes in Eurasian blackbirds, *Turdus merula* (Linnaeus), in relation to urbanisation assayed six established candidate genes *Clock*, *Adcyap1*, *NPAS2*, *CREB1*, *DRD4* and *SERT* (Mueller *et al.*, 2013*b*). The authors identified two *Clock* alleles, with the most common genotype being homozygous Q_7, while *Adcyap1* was considerably more diverse with almost 20 detected alleles. Transcriptomic analyses of 12 Eurasian blackbirds displaying differential resident *versus* migratory behaviour found several clusters of differentially expressed genes, however, none were circadian clock genes; one was associated with moult rate, which may influence migration timing (Franchini *et al.*, 2017). Although this study detected differential gene expression between two morphs within a sympatric population, the absence of relevant phenological functions for the identified genes makes interpretation difficult.

A candidate gene approach was applied to two congeneric species of bluebird: mountain bluebird, *Sialia currucoides* (Bechstein) and western bluebird, *Sialia mexicana* (Swainson) (Sauve *et al.*, 2021). *Adcyap1* and *DRD4* were assayed and correlations with migration phenology assessed; western bluebirds are partial migrants, often switching between strategies, while mountain bluebirds are obligate migrants. The analyses revealed a potential role for *DRD4*, a gene linked previously to exploratory behaviour in tits (Korsten *et al.*, 2010; Mueller *et al.*, 2013*a*) and swans (Van Dongen *et al.*, 2015), but absent in some warblers (Mueller *et al.*, 2011; Edwards *et al.*, 2015). No role was evident for *Adcyap1* (Sauve *et al.*, 2021) although less allelic diversity was found compared to studies which did find such a correlation (e.g. Eurasian blackcaps; Mueller *et al.*, 2011).

(*j*) *Shrikes and orioles (Families: Laniidae, Oriolidae)*

The Eurasian golden oriole, *Oriolus oriolus* (Linnaeus), and woodchat shrike, *Lanius senator* (Linnaeus), were included in a larger study evaluating inter-species differences in clock length polymorphisms (Bazzi *et al.*, 2016*a*) and three elements of migration phenology: migration date, migration distance, and latitude of breeding. Both orioles and shrikes had relatively short Poly-Q repeat regions with the most common allele being Q_6 and Q_9 respectively. How intra-species variation in the allelic diversity of these species is related to migratory strategy remains to be investigated.

(2) Non-passerine birds

(*a*) *Buzzards, hawks, and kites (Order: Accipitriformes, Family: Accipitridae)*

The Eurasian buzzard, *Buteo buteo* (Linnaeus), is monoallelic for the *Clock* allele, with all genotyped individuals homozygous for Q_8 (Chakarov *et al.*, 2013). The same study also assayed *Adcyap1*, *NPAS2*, and *CREB1* and found significant correlates with the observed polymorphisms in juveniles for timing of dispersal and dispersal distance. Interestingly no major differences were detected between the German ($N = 976$) and Bulgarian ($N = 23$) populations, indicating that population structure for gene polymorphisms is present even in smaller samples and that more extensive sampling may not significantly improve resolution. This study also included the red kite, *Milvus milvus* (Linnaeus), and northern goshawk, *Accipiter gentilis* (Linnaeus), but found no significant correlations with migration behaviour.

(*b*) *Hoopoes (Order: Bucerotiformes, Family: Upupidae)*

In Eurasian hoopoe, *Upupa epops* (Linnaeus), the most frequent allele for *Clock* was Q_8, although Q_7 was almost as common; calculated heterozygosity was 0.50. *Adcyap1* showed

comparable diversity with three alleles ranging in size from 157 to 159 bp and a higher calculated heterozygosity of 0.56 (Bazzi *et al.*, 2016*a*).

(*c*) *Wrynecks (Order: Piciformes, Family: Picidae)*

In the Eurasian wryneck, *Jynx torquilla* (Linnaeus), the most frequent allele size for *Clock* was the Q_8 allele. Four alleles were present ranging in size from Q_6 to Q_{10}; calculated heterozygosity was 0.44. Five *Adcyap1* alleles were identified, ranging in size from 131 to 137 bp, considerably shorter than those reported for most other non-passerines (Table 1). Calculated heterozygosity was considerably higher at an estimated 0.68 (Bazzi *et al.*, 2016*a*).

(*d*) *Bee-eaters (Order: Coraciiformes, Family: Meropidae)*

The European bee-eater was mono-allelic for *Clock* (Q_4 allele), considerably shorter than in most other non-passerines. For *Adcyap1* three alleles were identified, ranging in size from 155 bp to 169 bp. There was considerable homozygosity for the most common allele (163 bp), and an estimated diversity of only 0.19 (Bazzi *et al.*, 2016*a*). This study only included individuals from migratory European bee-eaters in Italy and did not include samples from the resident population found in South Africa.

(*e*) *Nightjars (Order: Caprimulgiformes, Family: Caprimulgidae)*

In the European nightjar, *Caprimulgus europaeus* (Linnaeus), the most common *Clock* allele was the Q_8 allele and two alleles were identified; calculated heterozygosity was 0.35 and most individuals were homozygous. A larger number of *Adcyap1* alleles were identified than in other non-passerine species (nine alleles) and a calculated heterozygosity of ∼0.81 (Bazzi *et al.*, 2016*a*).

(*f*) *Pigeons and doves (Order: Columbiformes, Family: Columbidae)*

In European turtle dove, *Streptopelia turtur* (Linnaeus), the most common allele size for *Clock* was the Q_7 allele, with a minimum of two alleles, but with a heterozygosity of 0.03 (i.e. they were nearly monoallelic). *Adcyap1* was more polymorphic with five alleles detected ranging in size from 148 to 152 bp. Overall diversity was relatively low with a calculated heterozygosity of 0.30 and many individuals homozygous for the most common 150 bp allele (Bazzi *et al.*, 2016*a*).

(*g*) *Gulls and shorebirds (Order: Charadriiformes, Families: Laridae, Scolopacidae, Charadriidae)*

Correlations of length polymorphisms in two regions of *Clock*, *Adcyap1* and *NPAS2* with laying date were studied in females of a large breeding colony of the largely resident yellow-legged gull, *Larus michahellis* (Naumann) (Romano *et al.*, 2018). Similar distributions of all assayed alleles were found between early- and late-laying birds, with the authors concluding that selection due to photoperiod on clock gene polymorphisms may not be universal in birds (Romano *et al.*, 2018). It should be noted that this study included only one of the two recognised subspecies, *L. m. michahellis*. Polymorphisms are likely to be more evident in early speciation (Rolland *et al.*, 2014), between ecological niches (Gómez *et al.*, 2016), or along lateral gradients (Linck, Freeman & Dumbacher, 2019).

The bar-tailed godwit subspecies *Limosa lapponica baueri* (Linnaeus) makes one of the most arduous annual journeys, breeding in Siberia and Alaska and overwintering in New Zealand. Parody-Merino *et al.* (2019) reported a high degree of *Clock* variability, with three nearly equally distributed alleles Q_9–Q_{11}. Statistical analyses revealed no clear relationship between allele size and timing of migration, but a slight latitudinal cline was observed with longer alleles tending to be found in individuals that travel further north. The authors concluded that clock gene polymorphisms are 'not a strong candidate for driving migration timing in migratory birds generally.' (p. 843), however, the fact that this species displayed significantly more heterozygosity than shorter range migrants should not be overlooked. Furthermore, this study only tested one distinct subspecies and may therefore have missed potential diversification among subspecies.

A recent study (de Almeida Miranda *et al.*, 2022) assessed diversity within *Adcyap1* in several species of shorebirds: the collared plover, *Charadrius collaris* (Vieillot), semipalmated sandpiper, *Calidris pusilla* (Linnaeus), semipalmated plover, *Charadrius semipalmatus* (Bonaparte), and spotted sandpiper, *Actitis macularius* (Linnaeus). They found several alleles for each species but the study was limited in its resolution by small sample sizes. Shorebirds represent a group with unique challenges in studying any underlying migration genetics as in many species their ranges are restricted to narrow strips along the coast of continents, with several occurring on both western and eastern coasts, in addition to several species following a distinct migration pattern along a flyway between Australasia and parts of the Nearctic. As such they are better suited to studies that track individuals using geolocators rather than studies using a more general approach with population-level averages for their range.

IV. CROSS-SPECIES COMPARATIVE ANALYSIS

(1) Population genetics

The results of the population genetics analyses are summarised in Table 3, with more detailed results available as online supporting information in Tables S1–S3. Across all 40 species included in this analysis, a total of 13 Poly-Q alleles was identified, ranging in size from Q_4 in the European bee-eater to Q_{16} in the blue tit, common redstart, and whinchat. Far more *Adcyap1* alleles were reported: 51 alleles ranging in size from 131 to 189 bp. The Hardy–Weinberg test showed that the *Clock* and *Adcyap1* alleles were in equilibrium for nearly all species, with only five species failing equilibrium assumptions in each case (Tables 3 and S1).

Table 3. Summary of results of population genetics comparative analysis testing of individual species for which allele data were available for *Clock* and *Adcyap1*. *, $P < 0.10$; **, $P < 0.05$; ***, $P < 0.02$.

Hardy–Weinberg	*Clock*			*Adcyap1*		
	N	Total	P	N	Total	P
In equilibrium	34	39	<0.02	32	37	<0.02***
Not in equilibrium	5			5		

Heterozygosity	*Clock*			*Adcyap1*		
	N	Total	H_o/H_e	N	Total	H_o/H_e
Observed (H_o) > Expected (H_e)	17	39	0.325/0.33	19	37	0.678/0.69
Expected (H_e) > Observed (H_o)	15			18		
Observed (H_o) = Expected (H_e)	3			–		
Single allele	4			–		

Neutrality (Ewens–Watterson)	*Clock*			*Adcyap1*		
	N	Total	P	N	Total	P
Neutral	32	39	>0.05	32	37	<0.05**
Selection	3			5		
Single allele	4			–		

Linkage disequilibrium	*Clock*	
	N	Total
Clock vs *Adcyap1*		
In equilibrium	33	36
Not in equilibrium	3	

The Hardy–Weinberg test on the entire data set also showed a lack of equilibrium ($P < 0.02$), as anticipated for species without known gene flow between them. Three species had equal observed (H_o) and expected (H_e) heterozygosity for the *Clock* allele while four species were mono-allelic (Table S1). For both alleles H_o was slightly higher than H_e in nearly half of the tested species: 17/39 for *Clock* and 19/37 for *Adcyap1*; mean H_o for the entire data set (Table 3) was 0.325 for *Clock* and 0.678 for *Adcyap1*, which was lower than the calculated expected heterozygosity (0.33 and 0.69, respectively).

The neutrality tests (Tables 3 and S2) detected significant evidence for deviation from neutrality in three out of 39 species for the *Clock* allele and for the *Adcyap1* allele. Overall tests for selection among species detected no evidence for deviation from neutrality in *Clock* but did detect deviation from neutrality for *Adcyap1*. For the 36 species for which data on both alleles were available, linkage disequilibrium was detected in only three species; the remainder appeared to be in equilibrium (Table S3).

(2) Mantel tests

A significant correlation was detected between the genetic distance (F_{ST}) of the *Clock* alleles and breeding latitude ($P = 0.099$), non-breeding latitude ($P = 0.018$), taxonomic distance ($P = 0.013$) and divergence time ($P = 0.051$) (Tables 4 and 5). Apart from divergence times, these correlations were positive. By contrast, no significant relationship was detected between F_{ST} for *Adcyap1* alleles and geographic attributes of migration phenology or taxonomic distance, but a significant negative correlation was found with divergence time ($P = 0.010$).

(3) Phylogenetic generalised least squares analyses

PGLS analyses did not find significant relationships between the average latitudes of breeding and non-breeding ranges and the allele length of the most common *Clock* or *Adcyap1* allele (Tables 4 and 5). The only significant relationship was between *Clock* allele length and total migration distance. Some correlations (at $P < 0.01$) were detected between *Clock* allele length and the start and middle dates of autumn migration when these dates were calculated relative to either the summer solstice or autumn equinox. A significant correlation was detected between *Adcyap1* and only the middle and end dates of spring migration and only when these were calculated in relation to the date of the winter solstice. The strength of the overall phylogenetic signal, assessed by estimating lambda and kappa, was strongly correlated with allele length of the most common alleles for both genes. A phylogenetic ANOVA between migratory and resident species

Table 4. Summary statistics for data used in the cross-species comparative analyses of the *Clock* and *Adcyap1* alleles (see Table 5). MYA, million years ago; PGLS, phylogenetic generalised least squares.

	Clock					*Adcyap1*				
Variable (x)	N	Mean	Std deviation	Minimum	Maximum	N	Mean	Std deviation	Minimum	Maximum
Mantel tests:										
Genetic distance (F_{ST})	39	1.54	1.98	0	9.42	39	37	1.96	0	2.23
Geographic distance (°):										
Breeding latitude	39	58.129	48.351	0	156.573	39	37	57.436	0	48.853
Non-breeding latitude	39	71.046	63.941	0	178.575	39	37	71.872	0	64.245
Taxonomic distance:	39	81.12	21.69	0	100.00	39	37	80.51	0	22.09
Evolutionary distance:										
Mean divergence times (MYA)	39	39.86	19.19	0	75.00	39	37	39.63	0	19.71
PGLS models:										
Migrants										
Allele size (*Clock* as Poly-Q, *Adcyap1* in bp)	58	9	2.22	4	14	58	54	166	135	9.60
Observed heterozygosity (H_o)	48	0.325	0.249	<0.001	0.839	48	39	0.670	0.191	0.179
Breeding latitude (°)	58	17.987	13.039	0.837	56.049	58	54	17.964	0.838	13.486
Non-breeding latitude (°)	58	48.429	9.741	4.669	66.762	58	54	47.549	4.669	14.537
Migration distance (m)	58	4,573,175	2,232,252	875,528	12,388,217	58	54	4,669,914	875,528	2,263,790
Migration distance (°)	58	41.018	19.934	8.250	111.290	58	54	41.873	8.250	20.240
Residents										
Allele size	18	10	1.94	8	14	18	17	170	139	13.55
Observed heterozygosity (H_o)	8	0.131	0.154	<0.001	0.343	8	2	0.538	0.312	0.319
Latitude (°)	18	23.876	17.396	2.419	55.384	18	17	24.457	2.419	17.751
Range (m)	18	691,024	727,105	10,531	2,657,515	18	17	715,938	10,531	741,522

Table 5. Summary of results of Mantel tests and phylogenetic generalised least squares (PGLS) regression analysis for *Clock* and *Adcyap1* alleles in the studied avian species (see Table 4 for summary of data used in the analysis). For Mantel tests, results are reported for tests for comparisons of the genetic distance (F_{ST}, see Table 4) between species with migration-related variables, taxonomic distance between species, and mean divergence times. For PGLS, the tests compared the length of the most common allele for each species to the migration-related variables shown. The strength of the phylogenetic signal for each gene was also assessed by estimating lambda and kappa. *, $P < 0.10$; **, $P < 0.05$; ***, $P < 0.02$.

Mantel tests	*Clock*			*Adcyap1*		
	Z-value	*P*-value	*R*-value	*Z*-value	*P*-value	*R*-value
Geography						
Breeding latitude	0.086	0.099*	1.638	0.036	0.499	0.657
Non-breeding latitude	0.124	0.018***	2.426	0.033	0.520	0.631
Taxonomy						
Taxonomic distance	0.116	0.013***	2.479	0.058	0.239	1.185
Evolutionary history						
Mean divergence time	−0.139	0.051*	−1.901	−0.190	0.010***	−2.573

PGLS		*P*	R^2	DF	*P*	R^2	DF
Geography							
Breeding latitude		0.275	0.02	74	0.300	0.02	69
Non-breeding latitude		0.220	0.03	56	0.472	0.01	52
Migration distance		0.093*	0.04	74	0.342	0.01	69
Timing							
Spring migration *versus*	Start	0.343	0.02	56	0.273	0.02	52
winter solstice (9:15 LD)	Mid	0.325	0.02	56	0.096*	0.05	52
	End	0.406	0.01	56	0.070*	0.06	52
Spring migration *versus*	Start	0.638	0.00	56	0.450	0.01	52
spring equinox (12:12 LD)	Mid	0.454	0.01	56	0.480	0.01	52
	End	0.389	0.01	56	0.532	0.01	52
Autumn migration *versus*	Start	0.077*	0.05	56	0.905	0.00	52
summer solstice (15:9 LD)	Mid	0.058*	0.06	56	0.643	0.00	52
	End	0.221	0.03	56	0.443	0.01	52
Autumn migration *versus*	Start	0.097*	0.05	56	0.950	0.00	52
autumn equinox (12:12 LD)	Mid	0.070*	0.06	56	0.602	0.01	52
	End	0.236	0.03	56	0.420	0.01	52
Phylogenetic signal							
Lambda (λ)		0.000***	0.92	74	0.000***	0.75	69
Kappa (κ)		0.001***	0.73	74	0.001***	0.61	69

revealed no significant partitioning based on *Clock* or *Adcyap1* allele length (data not shown) while the largely sedentary species complex of manakins had clock alleles ranging in size from Q_8 to Q_{11}, overlapping with those observed in migratory species.

(4) Time tree and palaeogeography

Divergence times for the main lineages of the species included in our analysis are represented in the reconstructed time tree (Fig. 7). The primary speciation event dividing the order Passeriformes from non-passerine birds took place around 85 MYA during the Late Cretaceous. The mean divergence time for the study species was ∼35 MYA with the most recent divisions taking place during the Miocene and Pliocene; the most recent speciation for this data set was at less than 1 MYA between two junco species.

According to palaeogeographic reconstructions (Fig. 7 and Video S1), the primary division between passerines and non-passerines occurred prior to the formation of most continents, and would likely have required several range shifts, which would only have occurred ∼50 MYA with a substantial amount of continental drift continuing until about 21 MYA when most continents started to assume their contemporary positions. There was still, however, a continuation of tectonic plate movement resulting in significant geographic remodelling on most continents, shaping the landscape within which range selection and speciation occurred.

V. DISCUSSION

Our systematic review of the existing evidence for a potential role of diversity within genes associated with the circadian clock machinery in regulating or shaping migration phenology clearly identifies conflicting evidence. Several studies have reported such relationships (Liedvogel *et al.*, 2009;

Caprioli *et al.*, 2012; Kuhn *et al.*, 2013) whilst others found no evidence for an association (Peterson *et al.*, 2013; Contina *et al.*, 2018; Parody-Merino *et al.*, 2019). Additionally, several transcriptomic studies on related species have detected no differences in expression levels of key clock genes (Jones *et al.*, 2008*a*; Franchini *et al.*, 2017; Brown, 2019) used in candidate gene association studies.

It should be noted that pitfalls within study design or data analyses could confound the results. For example, most early studies relied on the Mantel test (Mantel, 1967) to identify correlations between genetic distance and geographic distance, as is a common practice in studies of spatial genetics and ecology. More recently, however, several authors have questioned the suitability of the Mantel test in such applications (Guillot & Rousset, 2013; Legendre, Fortin & Borcard, 2015) as this test is designed to compare two distance matrices that both measure differences rather than physical distance and argued that geographic distance expressed in kilometres may exaggerate the relationship. Other potential confounding issues include the *post-hoc* grouping of study individuals based on observed outlier status (Bazzi *et al.*, 2015) or sex (Dor *et al.*, 2011) rather than predetermined grouping, small sample sizes (de Almeida Miranda *et al.*, 2022), and the averaging of alleles in heterozygotes to analyse mean allele length (Zhang *et al.*, 2017).

Analysing individuals by mean allele length makes several assumptions about the underlying biology of the system that have yet to be validated. Firstly, it assumes equal bi-allelic expression from a single locus, an absence of parental imprinting (Jang *et al.*, 2013), and identical regulation of both alleles. This contradicts the central hypothesis of altered entrainment cycles in the presence of a length polymorphism as well as some existing evidence for heritable patterns of methylation in birds (Romano *et al.*, 2017; Saino *et al.*, 2019). Secondly it assumes knowledge of the copy number variation for the studied genes (Skinner *et al.*, 2014), which may be particularly complex in birds given that different karyotypes where chromosome numbers ranging between 78 and 82 can be found in most species (Degrandi *et al.*, 2020). Initial studies grouped individuals based on homozygosity, presence of the most common allele, and heterozygosity with a longer or shorter allele to model likely gene effects without assuming equal bi-allelic expression from a single locus (Johnsen *et al.*, 2007).

Some studies may also have deviated by analysing total fragment length and including alleles that differed by only one base pair in the data set (Contina *et al.*, 2018), thereby not implicitly measuring only the identified length polymorphism, as well as including an excessively narrow cohort in the analysis by focusing on a single subspecies (Parody-Merino *et al.*, 2019). The central hypothesis tested in such studies is that genetic differences establish a migratory divide that leads to speciation; how variation within a single subspecies fits into this hypothesis is unclear as speciation is unlikely to be documented below the subspecies level. Additionally, in many of the studied species for which known subspecies exist, no clear effort was made to assign individuals to specific subspecies, but rather the assumption was that all individuals at the same study site would belong to a single subspecies. The importance of accounting for subspecies has been highlighted by the increasing number of documented cases of hybrid speciation among birds, including eagles (Väli *et al.*, 2018), finches (Lamichhaney *et al.*, 2018), manakins (Barrera-Guzmán *et al.*, 2017), sparrows (Hermansen *et al.*, 2011), warblers (Brelsford, Milá & Irwin, 2011; Ralston, Ermacor & Kirchman, 2015) and tits (Janas *et al.*, 2021).

Most studies published to date were conducted at the species level and have focused on European species of birds within the order Passeriformes. The name 'Passeriformes' was derived from the Latin *passer*, meaning sparrow, while the French verb *passer* refers to movement (Vieillot, 1816). As many French naturalists contributed to early ornithological works, Vieillot (1816) noted that some scientists may have had a mistaken sense that passerines were migratory while non-passerines were sedentary by conflating these words in early ornithological works like the *Histoire Naturelle* (Leclerc, 1780). This may have established a persistent subconscious bias considering most of the early works were written in either Latin or French. Other potential reasons for a focus on passerines in migration research could include their suggested higher diversification, and possibly speciation rates (Jetz *et al.*, 2012; Prum *et al.*, 2015), differences in appropriate trapping methods, or a perception that they have more complex migration strategies. However, mist-net trapping can be used effectively used in many non-passerine species including kingfishers (Dalton *et al.*, 2022), cuckoos (Chaisi *et al.*, 2019), fluff-tails (Dalton *et al.*, 2016), and hornbills (Theron *et al.*, 2013), and some exceptional long-distance migrations are found in non-passerine species (Parody-Merino *et al.*, 2019).

The full data set for *Clock* revealed a limited number of genotypes with a small number of alleles and widespread homozygosity while *Adcyap1* was considerably more diverse with many more genotypes per species and more heterozygotes. A general trend was found for higher observed than expected heterozygosity among nearly half of the species (Table S1) while the whole data set analysis showed only marginally less heterozygosity (Table 3). Population genetics analyses found most tested species to be in Hardy–Weinberg equilibrium, with only five species failing equilibrium assumptions. For the willow warbler and common chiffchaff, this was anticipated as their data included individuals of known subspecies. For the remainder, it is possible that a similar population substructure exists or that there are heterozygote deficiencies or advantages potentially arising from a variety of factors such as inbreeding, hybridisation or recent population bottlenecks (Hedrick, 1987; Lade *et al.*, 1996; Luikart & Cornuet, 1998).

Our comparative analysis found a significant correlation between *Clock* alleles and both breeding and non-breeding latitudes using Mantel tests, but not PGLS (Freckleton, Harvey & Pagel, 2002), with concerns regarding false positives arising from use of the Mantel test in spatial genetics potentially an explanation (Guillot & Rousset, 2013; Legendre *et al.*, 2015). No correlations with these variables

were found for *Adcyap1* using either method, although this may be due to the difficulty in comparing this gene across taxa in the absence of sequence data, as our use of the full length of the allele may result in inclusion of length variation in non-focal regions (Bazzi *et al.*, 2016*a*). Additionally, no evidence was found for partitioning migratory and sedentary species based on either candidate gene, consistent with previous findings using phylogenetic approaches (Lugo Ramos *et al.*, 2017). When specifically analysing the relationship between alleles and the timing of migration among migratory species, the results weakly supported a correlation between *Clock* alleles and the timing of autumn migration (Ralston *et al.*, 2019; Justen *et al.*, 2022) while for *Adcyap1*, there was weak evidence for a relationship with the timing and staging of spring migration (Bazzi *et al.*, 2016*a*; Ralston *et al.*, 2019).

Interestingly, an analysis of genetic distance in relation to divergence times found a significant correlation for both *Clock* and *Adcyap1* alleles, as well as a relationship between taxonomic distance and *Clock* alleles, indicating that contemporary genotypes may still resemble the ancestral genotypes inherited millions of years ago. This was further supported by a strong phylogenetic signal for both genes, indicating that closely related species have similar allele lengths, and that variation is best explained by lineage, similar to previous findings (Bazzi *et al.*, 2016*a*). This also supports findings from European pied flycatcher studies that identified similar alleles in contemporary (Saino *et al.*, 2015*a*) and historical samples (Kuhn *et al.*, 2013). Considering the palaeogeographic remodelling which coincided with the divergence of these lineages over the past 85 million years, along with global climatic changes, selective sweeps and convergent evolution would have abrogated this relationship if these genes were under strong selection in terms of adapting migration strategies in response to geographic or environmental changes (Stern, 2013). In the comparative analysis, the tests for deviation from assumptions of neutrality and evidence of selection failed to detect selection in either gene for most species.

A substantial amount of genetic research in ornithology from the 1990 s (Vos *et al.*, 1995) to shortly after the turn of the century (Bensch & Åkesson, 2005) focused on identifying genes with length polymorphisms that co-vary with latitude (Bensch, Åkesson & Irwin, 2002) and could be used as molecular markers in population assignment or barcoding (Ottvall *et al.*, 2005). This included the identification of several markers that have been used successfully for population assignment in species such as willow warbler (Bensch *et al.*, 2002), house wren, *Troglodytes aedon* (Vieillot) (Arguedas & Parker, 2000), superb fairy-wren (Double *et al.*, 1997), and long-tailed manakin, *Chiroxiphia linearis* (Bonaparte) (McDonald & Potts, 1994). Therefore, although some evidence exists that polymorphisms within the tested candidate genes *Clock* and *Adcyap1* co-vary with migration behaviour, considering similar relationships (such as latitudinal clines in allele length within ranges and an influence on timing of breeding) was also illustrated in several sedentary species (Johnsen *et al.*, 2007; Liedvogel *et al.*, 2012), caution should be applied when translating these findings into a causal relationship.

Future studies are currently needed in the field of migration genetics to address current gaps in our understanding of the regulation of the circadian machinery. Such studies should ideally expand the breadth of species for which data are available, include transcription data comparing expression levels and dominance of alleles in heterozygous individuals, compare expression levels among species with known polymorphic length variation in candidate genes, determine the copy number variation of circadian genes in avian species, and use information on epigenetics to address any potential roles in regulating these genes. Future studies should, ideally, be designed to avoid the limitations identified above, including appropriate sample sizes, sampling to capture as much variation in migration strategies as possible, controlling for subspecies status in sample populations, the use of correct taxonomy, the inclusion of non-passerines, and data analysis procedures that make the fewest assumptions about the regulation and expression of heterozygous alleles.

VI. CONCLUSIONS

(1) Some evidence exists that polymorphisms within the poly-Q region of the *Clock* gene are related to geo-spatial differences in the range of migrating birds, as well as the timing of Autumn migration.
(2) Little evidence exists that polymorphism expressed as total allele length of *Adcyap1* has a geo-spatial pattern, however there is weak evidence for a relationship with the timing of spring migration.
(3) Both *Clock* and *Adcyap1* have a strong phylogenetic signal indicative that alleles and genotypes are highly heritable within lineages.
(4) For both *Clock* and *Adcyap1* the observed patterning is well correlated to divergence times and may therefore still reflect the ancestrally inherited genotypes rather than recently acquired changes.
(5) No clear evidence exists that either candidate gene can be used to distinguish migratory from sedentary birds across all taxa.

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VIII. DATA AVAILABILITY STATEMENT

Data used in this study are available for download from the Zenodo repository at: https://doi.org/10.5281/zenodo.6637839. The custom-designed python script PAReTT version 1.0.1 is available for download for installation from source code on GitHub (https://github.com/LSLeClercq/PAReTT).

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Heterozygosity and Hardy–Weinberg equilibrium test results for *Clock* and *Adcyap1* alleles for 40 avian species.

Table S2. Fixation index and Ewers–Waterson test results for *Clock* and *Adcyap1* alleles for 40 avian species.

Table S3. Linkage disequilibrium test results comparing *Clock versus Adcyap1* alleles for 36 avian species.

Video S1. Reconstruction of paleogeography relevant to the major periods of divergence indicating the differences between contemporary and historical landscapes of evolution and selection.

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