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Physiology

Extraordinarily rapid proliferation of cultured muscle satellite cells from migratory birds

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Migratory birds experience bouts of muscle growth and depletion as they prepare for, and undertake prolonged flight. Our studies of migratory bird muscle physiology *in vitro* led to the discovery that sanderling (*Calidris alba*) muscle satellite cells proliferate more rapidly than other normal cell lines. Here we determined the proliferation rate of muscle satellite cells isolated from five migratory species (sanderling; ruff, *Calidris pugnax*; western sandpiper, *Calidris mauri*; yellow-rumped warbler, *Setophaga coronata*; Swainson's thrush, *Catharus ustulatus*) from two families (shorebirds and songbirds) and with different migratory strategies. Ruff and sanderling satellite cells exhibited rapid proliferation, with population doubling times of 9.3 ± 1.3 and 11.4 ± 2 h, whereas the remaining species' cell doubling times were greater than or equal to 24 h. The results indicate that the rapid proliferation of satellite cells is not associated with total migration distance but may be related to flight bout duration and interact with lifespan.

1. Introduction

Migratory birds typically undertake multi-hour flights with some species, particularly shorebirds, taking this strategy to the extreme and staying aloft as long as 9 days in a single flight bout [1]. Migration requires physiological preparation including muscle hypertrophy, and flight muscles are also damaged and catabolized for fuel during flight [2–4]. While all migratory birds undergo physiological preparations, species that engage in very long continuous flight bouts exhibit especially rapid muscle growth in advance of their flights. The red knot (*Calidris canutus*) increases muscle mass at a rate of 1.7% per day over one week at stopover between multi-day flights [5] in comparison to 0.2% per day muscle volume increase in humans engaged in an intensive resistance exercise programme [6]. Muscle growth and repair during migration is driven by hypertrophy and supported by the proliferation of satellite cells, which contribute nuclei to growing muscle cells [7,8]. Cell proliferation rate is a fundamental aspect of cell culture studies that influences study design and can provide insight into cellular and organismal physiology. Proliferation rates are influenced by extrinsic (e.g. growth factors, micro-RNAs, media conditions) and intrinsic (e.g. genetic, cell type) factors that ultimately influence the rate that cells progress through the cell cycle [9].

Our interest in the physiology and energetics of migratory birds recently led to studies in which we compared the metabolism of muscle cells cultured from medium-distance migratory songbirds (yellow-rumped warbler; *Setophaga coronata*) to a species of long-distance migratory shorebird (sanderling; *Calidris alba*) [10]. This work was completed using skeletal muscle satellite cells, a

Table 1. Cell lines and primary cells described in the literature and their estimated doubling times.

cell name	cell type	species	doubling time (h)	reference
primary cells	skeletal muscle satellite cells	ruff (Calidris pugnax)	7.9 ± 1.2	present study
primary cells	skeletal muscle satellite cells	sanderling (Calidris alba)	8.6 ± 0.9	present study
RAW264.7	leukaemic monocyte macrophage	mouse (Mus musculus)	11	[13]
L5178Y	lymphoma	mouse	11.5	[14]
primary cells	skeletal muscle satellite cells	western sandpiper (Calidris mauri)	18.1 ± 2.8	present study
T24	astrocytoma glioma line	rat (Rattus norvegicus)	18.2	[15]
primary cells	primary embryonic muscle — Hy-line chickens	chicken (Gallus gallus)	20	[16]
primary cells	cornea endothelial	bovine (Bos Taurus)	20–24	[17]
primary cells	skeletal muscle satellite cells	rat	21	[18]
3T3	embryonic fibroblast	mouse	21.8	[19]
HeLa	cervix adenocarcinoma	human (Homo sapiens)	24.1	[19]
HL-60	acute promyelocytic leukaemia	human	25	[20]
primary cells	skeletal muscle satellite cells	Swainson's thrush (Catharus ustulatus)	25.3 ± 2.3	present study
primary cells	skeletal muscle satellite cells	yellow-rumped warbler (Setophaga coronata)	25.4 ± 5.6	present study
F98	undifferentiated glioma clone	rat	26.1	[15]
D74	differentiated glioma clone	rat	26.7	[15]
primary cells	primary embryonic muscle — Welp chickens	chicken	26.9	[16]
A549	lung epithelial carcinoma	human	27	[13]
T22	spongioblastoma glioma line	rat	27.5	[15]
L929	fibroblast	mouse	28	[13]
primary cells	skeletal muscle satellite cells	pig (Sus scrofa)	28	[21]
Jurkat	T-cell leukaemia	human	30	[20]
KG-1a	acute myelogenous leukaemia	human	31	[20]
T9	anaplastic glioma line	rat	31.8	[15]
primary cells	glia	rat	34.2	[15]
MCF-7	breast adenocarcinoma	human	35	[20]
K562	chronic myelogeneous leukaemia	human	42	[20]
ARPE-19	normal retinal epithelia	human	55	[13]
22Rv1	prostate carcinoma	human	63	[13]

type of adult stem cell that contributes nuclei to established or new muscle fibres, and ultimately muscle growth [11,12]. During the study, we noticed that the sanderling cells proliferated approximately three times faster than the warbler cells; rates that were unlike those described previously in other normal vertebrate muscle cells and comparable to rates documented in cancer cell lines (table 1) [13].

Our serendipitous finding led us to propose two alternative hypotheses for the remarkably rapid proliferation rate of sanderling muscle cells: (i) it may relate the ability of shorebirds to survive and recover rapidly from ultra-endurance flights lasting as long a week or more (phylogenetic hypothesis) or (ii) it may be a characteristic of long-distance migrant bird species independent of phylogenetic lineage (migration strategy hypothesis). In this study we measured the proliferation rates of satellite cells from three shorebird species and two songbird species that vary in migration strategy summarized in table 2. Under the phylogenetic hypothesis we predicted that the three shorebird species would exhibit rapid proliferation rates compared to the songbirds. Conversely, we predicted that proliferation rates may correspond to migration strategies such that species that migrate longer total distances and engage in longer flight bouts will exhibit more rapid proliferation.

2. Methods

This research was designed following the Canadian Council on Animal Care guidelines and all animal related procedures were approved by the Western University Animal Care Committee (Protocol 2010-216). Wild birds were caught with the approval of the Canadian Wildlife Service (CA-0256 and 15-SK-SC004). Yellow-rumped warblers and Swainson's thrushes (Catharus ustulatus) were caught at Long Point, Ontario, Sanderlings were captured at Chaplin Lake, Saskatchewan, western sandpipers (Calidris mauri) were captured at Boundary Bay, British

Table 2. Migration and flight strategies of species that muscle satellite cells were isolated from.

species and references	total migration distance estimate	flight strategy
yellow-rumped warbler (*Setophaga coronata*) [22,23]	approximately 3500 km	nocturnal flights (>8 h)
Swainson's thrush (*Catharus ustulatus*) [23,24]	approximately 5000 km	nocturnal flights (>8 h)
western sandpiper (*Calidris mauri*) [25,26]	3000–10 000 km	typically short-hop 12–24 h but capable of ~40 h flights
sanderling (*Calidris alba*) [27–29]	3000–10 000 km	long-hop, 4–7 day flights (approx. 1600 km)
ruff (*Calidris pugnax*) ([30], B. Kempenaers 2021, personal communication, [31])	3000–10 000 km	short- and long-hop multi-day flights to cross ecological barriers (>4000 km)

Columbia, and ruffs (*Calidris pugnax*) were provided from a captive flock at Simon Fraser University, British Columbia. All birds were transported to the Advanced Facility for Avian Research at Western University, London, Ontario and housed in open aviaries (warblers and thrushes) or specialized shorebird rooms (sanderlings, sandpipers, and ruffs). Muscle satellite cells were isolated following methods described by Young *et al.* [10]. Cells were isolated from birds caught during migration shortly after entering captivity in autumn while still in a migratory state (western sandpiper, Swainson's thrush), when photostimulated into a migratory state in spring (yellow-rumped warbler, sanderling), and in natural daylength non-migratory wintering state (ruff). Sampling periods were selected in part for convenience around minimally invasive studies (e.g. blood sampling). Each cell isolate was derived from 2 g of muscle tissue and followed the same growth, freezing and thawing process. Cells were split and plated using the same media formula (10% chicken serum, 10% horse serum, 1% antibiotic–antimycotic, 0.1% gentamycin and 20 ng ml^{-1} basic fibroblast growth factor (bFGF) in McCoy's 5A media) and in the same proportions to maintain consistent cell passaging across species.

Following our early observations of some species' satellite cell growth, shorebird cells were counted over 4 days (6, 12, 18, 24, 36, 48, 72, 96 h) whereas those from songbirds were counted over 8 days (24, 48, 96, 144, 192 h). These primary satellite cells are grown with bFGF to prevent differentiation, however bFGF can increase the proliferation rate of muscle satellite cells [32,33]. Thus, we compared the proliferation rate of satellite cells with and without bFGF included in the media to examine proliferation under both conditions.

Cells thawed from liquid nitrogen were plated onto 100 mm collagen-coated cell culture dishes. Upon reaching 80% confluence, these cells were trypsinized (0.25% trypsin), and 20 000 cells were plated onto 35 mm collagen-coated plates in duplicate for each time-point to be counted. At each time-point, cells were trypsinized, centrifuged for 10 min at 800*g* in 1.5 ml tubes, and resuspended in media for counting. Ten microlitres of each cell suspension and 10 μl of trypan blue were combined and 10 μl of this counting suspension was added to a haemocytometer for counting. Cells were manually counted on the haemocytometer, blinded to the individual and treatment, and were converted to the total number of cells in each plate. Although we cannot test for the effect of seasonality, due to the isolation process, culturing for multiple generations and uniformity of culture media across species tested it is unlikely that sampling period had a significant impact on these results.

Doubling times of cells for each individual were determined by finding the maximum growth rate from the log-linear phase of growth curves and converting that value (μmax) to doubling time. We tested for differences among species and bFGF treatment combinations using ANOVA including the interaction between bFGF treatment and species. Pairwise differences were compared using Tukey's method. Analyses were completed in R v. 4.0.3 using the growth rates package for calculating maximum growth rates [34,35].

3. Results

The residuals of models including Swainson's thrush doubling times without bFGF were non-normal on both the natural (mean ± s.d.: 856.5 ± 338.9 h) and log scale. We removed this group from the analysis because these cells did not achieve log-linear growth within the 8 day period they were counted. The interaction between species and bFGF treatment was not significant ($F_{3,29} = 1.44$, $p = 0.25$) and was removed from the model. The bFGF treatment reduced doubling time ($F_{1,32} = 6.79$, $p = 0.014$), and there were differences among species ($F_{4,32} = 19.81$, $p < 0.0001$; figure 1). Pairwise comparisons split species into two groups of fast and slow growing satellite cells with ruff (bFGF−: 9.3 ± 1.3 h; bFGF+: 7.9 ± 1.2 h) and sanderling cells (bFGF−: 11.4 ± 2.0 h; bFGF+: 8.6 ± 0.9 h) having similar doubling times ($p = 0.99$) but both differed from all others ($p < 0.05$). Likewise, western sandpiper (bFGF−: 29.1 ± 8.9 h; bFGF+: 18.1 ± 2.8 h), yellow-rumped warbler (bFGF−: 29.1 ± 9.9 h; bFGF+: 25.4 ± 5.6 h) and Swainson's thrush cells (bFGF−: 25.3 ± 2.3 h) all had similar doubling times ($p > 0.05$). The rapid doubling times of ruff and sanderling satellite cells resemble those of the fastest growing immortalized cancer cells, whereas western sandpiper, yellow-rumped warbler and Swainson's thrush cells have doubling times within the apparent normal range of those described in embryonic poultry and mammalian studies (table 1).

4. Discussion

The rapid growth of sanderling and ruff skeletal muscle satellite cells are among the fastest growing vertebrate cell lines (table 1). Furthermore, the growth of these shorebird cells is especially interesting because primary cells typically proliferate slower than cell lines, which possess mutations in cell-cycle checkpoint pathways that immortalize cells and increase proliferation rate [36]. Given that the rapid proliferation of satellite cells was measured across eight individuals from two species (ruff and sanderling), it is unlikely that mutations that generate immortal cell lines contributed to these results.
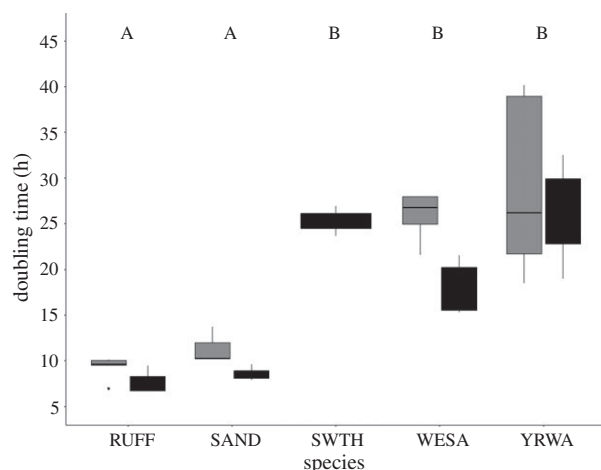
Figure 1. Doubling times of muscle satellite cells isolated from five species of migratory bird (Ruff, RUFF, $n = 5$; sanderling, SAND, $n = 3$; Swainson's thrush, SWTH; western sandpiper, WESA, $n = 5$; and yellow-rumped warbler, YRWA, $n = 5$) treated with (black) or without bFGF (grey). Boxplots represent the interquartile range with the centre line indicating the median value. Boxplot whiskers extend to 1.5 times beyond the interquartile range with individual points indicating values outside of that range. Doubling times were determined using the log-linear phase of growth from cells counted using a haemocytometer. ANOVA including species and bFGF treatment indicate that there are differences in doubling time among species ($p < 0.0001$) and between treatments ($p = 0.13$) with no interaction ($p = 0.25$). Differences among species are indicated with letters at the top.

Although we cannot present a definitive mechanism responsible for the rapid proliferation rates of sanderling and ruff muscle satellite cells here, evidence from the literature and our species comparison indicate there may be multiple factors driving these patterns and that these models may be useful for studying the physiology of ageing, muscle structure and satellite cell function more broadly.

Neither phylogeny nor migratory strategy appear to fully explain the variation in muscle satellite cell proliferation rates of the migratory birds we studied. With respect to phylogenetic history, the two passerines (thrush and warbler) proliferated slowest with Swainson's thrush cells exhibiting very limited growth without bFGF. However, the western sandpiper proliferated at a similar rate to the passerines, and is in the same genus (*Calidris*) as the sanderling. With respect to migratory strategy, the yellow-rumped warbler is the shortest distance migrant in our sample, breeding in the Canadian boreal forest and wintering in the mid-southern USA, whereas the Swainson's thrush is a long-distance neotropical migrant that winters in Central and South America with both passerines making nocturnal migratory flights (approx. 10–18 h) [22,37]. Like Swainson's thrush, the western sandpiper winters in Central and South America and generally migrates in 'short-hops' to the Arctic breeding grounds, although they are capable of non-stop flights greater than 40 h [25]. Nearctic breeding sanderlings are long-distance migrants that winter in central-southern South America [27]. However, sanderlings make use of limited stopover sites throughout their migrations, making longer flights between coastal or inland sites to reach their destinations, spending long periods of time at their stop-over sites [28]. In the Pacific basin, sanderlings are known to make non-stop flights as long as 6 days [38]. The ruff is also a long-distance migrant, wintering primarily in West Africa and migrating to the Eurasian Arctic to breed [39]. Ruffs

wintering in Africa cross the Sahara desert to reach staging areas in Europe [30]. A larger taxonomic comparison would provide more robust evidence, however our results provide some support for the hypothesis that individual migratory flight bout distance may be related to muscle satellite cell doubling time. Sanderling and ruff typically make extended flight bouts during their migrations, whereas yellow-rumped warblers and Swainson's thrush are primarily nocturnal migrants, and western sandpipers use a 'short-hop' strategy during their migration. Although we did not examine the role of lifespan specifically, it may be another factor, perhaps interacting with migratory flight, which could influence the proliferative potential of skeletal muscle cells in some birds.

In general, the lifespan of birds is greater than that of similarly sized mammals despite their relatively fast metabolisms [40]. Birds exhibit markers of ageing like shortening telomeres [41] and decreased resting metabolic rates [42]. However, there is no strong evidence for performance-based declines in long-lived birds, but instead these birds may suffer from catastrophic senescence as a result of the rapid failure of physiological systems resulting in death [43]. Long-lived seabirds (thick-billed murres, *Uria lomvia* and black-legged kittiwakes, *Rissa tridactyla*) do not exhibit age-related declines in muscle fibre cross-sectional area [44,45] that occurs in humans and other mammals [46–48]. Decreasing myonuclear domain (MND; i.e. cell volume regulated by each nucleus) with age may be one mechanism through which thick-billed murres are able to maintain muscle function late in life and satellite cells are responsible for contributing nuclei to muscle fibres [44,49,50]. MND size is important for maintaining transcriptional control and protein turnover in muscles and ultimately mechanical and metabolic function after growth by hypertrophy [51,52]. The contribution of nuclei to muscle by satellite cells in relation to hypertrophy is integral to their role in muscle function [53]. Although the species in the present study do not live as long as the seabirds described above, satellite cells from longer lived species in our sample proliferated at the fastest rates. Sanderlings have been recorded living up to 18 [54], and ruffs 14 years in the wild [41,55] or up to 20 years in captivity (D.B. Lank 2021, personal communication), whereas the remaining three species all have maximum recorded ages in the wild of less than or equal to 10 years: western sandpiper, nine years [56]; Yellow-rumped Warbler, seven years [57] and Swainson's thrush, 10 years [57]. While the precise ages of the wild-caught birds included in this study are not known (at least 1–2 years at the time of cell isolation), the captive-bred ruffs were remarkably old (6–14 years) considering their very rapid cell proliferation rate. Medium to large bodied ultra-endurance migratory birds, such as bar-tailed godwits (*Limosa lapponica baueri*) also have high survival rates and long lifespans [58], and perhaps extreme muscle regenerative capacity is a component of this migratory syndrome.

While we recognize the limitations of making strong inferences from the comparisons in this limited study, we have discovered that some birds exhibit very rapid muscle satellite cell proliferation rates that warrant further investigation. Similar studies of a broader, more diverse set of species and detailed examinations of the mechanisms driving the rapid doubling times of some bird muscle satellite cells are needed. Furthermore, satellite cells are completely unstudied in the context of migration, and basic studies of satellite

cell distribution, number and activation in the muscle of birds during their dramatic transitions could provide valuable insight into the flexibility of these phenotypes. The idiosyncratic timing of cell isolations examined in the present study did not reveal doubling time patterns associated with the timing of isolation in relation to their migratory condition (i.e. migratory condition sanderlings exhibited similar proliferation to wintering ruffs). However, muscle growth associated with migration may relate to the activity of satellite cells. Because it remains unclear if the isolated cells in the present study continue to exhibit seasonal phenotypes *in vitro*, further comparisons of satellite cell physiology within species across the annual cycle are warranted. Finally, because such rapid proliferation rates have not previously been described from cells in a non-cancer state, studying the mechanisms responsible for these phenomena may improve understanding of age-related muscle loss (sarcopenia), or more broadly, the limits of adult stem cell proliferative potential [47,50].

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