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Article

Avian migrants encounter higher temperatures but continue to add mass at an inland stopover site in the Great Lakes region

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As the climate changes, mismatches in phenology between predator and prey species may become more common. For example, many songbirds rely on short peaks in insect and fruit production at stopover sites during migration. Previous research indicates that migratory songbirds are able to modify their departure and arrival dates to some extent despite their reliance on more stable cues such as photoperiod and more stable endogenous factors. However, insect and plant phenology may shift more rapidly with changing climate, reducing foraging opportunities along migratory routes. To quantify changes in songbird arrival patterns at stopover sites during fall migration we analyzed forty years of banding data in nine passerine species commonly captured at banding stations in southwestern Michigan. Weather data revealed that the region has warmed by nearly 2° (C) over this timeframe. For each species, we assessed annual trends in arrival date and temperature at arrival. To determine whether arrival trends impacted stopover site function we also quantified trends in site use and morning mass gain. Arrival dates advanced significantly in three species, and were delayed significantly in three other species. However, air temperature at arrival increased significantly over time for all nine study species. Over the same time period, site use and the pattern of morning mass gain remained stable or increased for all species. Despite the changing climate and the resulting increase in temperature at arrival for migrants, our data indicate that these stopover locations continue to function as a refueling sites. Nonetheless, we must be wary of thresholds and ecological mismatches that may occur if warming trends continue.

Keywords: adapt, band station, climate, thrush, warbler, weight

The physical environment of our planet is changing at an increasing pace, due in large part to human activity (Grimm et al. 2008). For example, change in climate is often linked to degradation of the natural world because it alters key physical characteristics, such as temperature and precipitation (Trenberth 2011). Climate change is also known to impact the phenology of many organisms (Parmesan and Yohe 2003, Root et al. 2003), including plants (Jump and Peñuelas 2005) and insects (Deutsch et al. 2008), which serve as primary food sources for other organisms, such as songbirds (Crick 2004,

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Gallinat et al. 2015, Parris 2016). Like climate, the behavior and life histories of songbirds are rarely static (Gotthard and Nylin 1995, Marsh and Trenham 2008). However, the speed of adaptive change in birds is often limited by genetics (Hoekstra 2006) and stabilizing selection (Hansen and Houle 2004). As a result, the ability of many species to adapt rapidly to anthropogenic changes is in question.

Migration is a particularly critical period for songbirds, where changes in climate can lead to phenological mismatches (Emmenegger et al. 2016) and food shortages that reduce the likelihood that birds will thrive or even reach their wintering or breeding grounds (Hutto 1998). For example, insectivorous migrants that use Dutch forests characterized by a strong seasonal foraging peak have suffered steeper population declines as spring temperatures warmed than residents or migrants using more seasonally stable habitats (Both et al. 2010). Insect emergence, which creates critical food resources for migrating birds, is strongly tied to acute weather conditions (Both 2011, Forrest and Thomson 2011), which may lead to advancing windows of peak abundance under warmer conditions. In contrast, migratory timing in many bird species is mediated by more rigid endogenous circannual rhythms and stable external cues, such as the photoperiod (Berthold 2001, Cohen et al. 2015, Akesson and Helm 2020). Phenological mismatches between migratory songbirds and their food sources, including insect prey and plant material, may be particularly problematic at stopover sites where birds rest and refuel in route (Kaiser 1999) because foraging opportunities often serve as limiting factors (Bibby and Green 1983, Smith et al. 2007, Ferretti et al. 2019).

Recent studies indicate that neotropical migrants are able to modify the timing of their migration to some extent as temperatures warm (Bitterlin and Van Buskirk 2014, Usui et al. 2017). Many species are arriving earlier on their breeding grounds (Zelt et al. 2017), and leaving earlier, or later, in the autumn (Jenni and Kéry 2003, Mezquida et al. 2007, DeLeon et al. 2011). Although stopover habitats are used by most migratory songbirds, fewer studies have examined long-term changes in arrival timing at stopover sites as the climate changes. Since several factors can influence the speed of movement along the migratory route (Alerstam 2003, Paxton and Moore 2017), this is not a trivial question. Migratory birds could feasibly speed up or slow down progress to maintain consistent arrival times at stopover locations. Alternatively, birds might alter timing to arrive within more consistent arrival air temperatures.

In turn, arrival timing may impact the functionality of a stopover site. Stopover locations may be reused annually (Hasselquist et al. 2017), but changes in departure timing from the breeding grounds or altered flight speed might impact the use of particular locations. For example, birds moving more quickly along their migratory route might eliminate some stops, or choose alternative locations. Energetics at a stopover site may also be impacted. Because the energetic requirements during migration are substantial (Klassen 1996), mass gain is essential at stopover sites (Wolfson 1945, Schaub et al. 2008). At a successful stopover site, birds will gain mass over the progression of the morning after the nighttime fast – which may have included an energetically expensive flight during the evening prior to arrival (Dunn 2002, Bonter et al. 2007). Birds must also put on additional mass during each successive morning to prepare for their next flight (Nisbet et al. 1963, Moore and Kerlinger 1987). Thus, assessing whether birds continue to gain mass over the morning hours, or across successive days, can indicate whether the quality and function of a stopover site is changing over time. Since a very small percentage of birds are recaptured within a stopover visit, it is difficult to assess individual weight gain directly. However, assessing whether individuals captured throughout a morning become heavier as the morning progresses has been used regularly and successfully as a good measure of energetics at stopover sites (Mueller and Berger 1966, Winker et al. 1992, Morris et al. 2013).

One of the best available long-term sources of information on stopover arrival dates, capture rates and mass is the annual banding effort that takes place at many stopover locations at the same time and location during the fall migration each year (Morris et al 2013). We used forty years of banding data (1975–2015) collected during fall migration for nine migratory species from two stopover sites in Kalamazoo County, Michigan, to evaluate annual changes in 1) arrival dates, 2) temperature at arrival, 3), capture rate and 4) mass gain over the morning. To determine whether local climate also changed over this period we analyzed daily weather data during the data collection period. Based on warming trends observed in other climatic models (Randall et al. 2007), we predicted that temperature would increase over this time period. Given the known impacts of temperature on plant and insect phenology, we predicted that migrating birds would alter their arrival times to maintain a stable air temperature upon arrival at the stopover site. If migrants were unable to maintain a stable arrival temperature, we predicted that site use, as assessed through capture rate, might decline and that mass gain in individuals using our sites would be altered.

Methods

Study sites

Banding and data collection took place at two locations in Kalamazoo County: The Kalamazoo Nature Center (KN, ~8 ha) which is located 8 km directly north of the city of Kalamazoo (42.3635° N, 85.5902° W) and the Pitsfield Banding Station (PF, ~10 ha) which is located about 19.5 km south of the city of Kalamazoo (42.10° N, 85.30° W). The two stations were separated by 22.4 km. Banding data utilized from the Kalamazoo Nature Center was collected from 1975 to 2015. Mass was not recorded until 1985, limiting our mass analysis to data from 1985 to 2015. The Pitsfield Banding Station was opened in 1990 and data was utilized from 1990 to 2015.

Both banding sites are comprised of hardwood forests in mid-late succession. Native species include black oak *Quercus velutina*, white oak *Q. alba*, sugar maple *Acer saccharum*, red maple *A. rubrum*, black cherry *Prunus serotina*, eastern cottonwood *Populus deltoides*, black locust *Robinia pseudoacacia*, chokecherry *Prunus virginiana*, assorted aspen *Populus* spp. and willows *Salix* spp. In both locations non-native species are removed annually, including autumn olive *Elaeagnus umbellata*. The lanes surrounding mist nets have been managed to ensure that nearby vegetation is ~10 m in height. Adjacent landscapes are a mix of residential development, agricultural fields and hardwood forests.

Study species

We selected nine bird species for analysis because they were non-resident during the breeding season or winter months, and were among the species captured most often and most regularly at both stations (> 1000 total individuals, > 25 individuals year^{-1}). Our species included; the gray-cheeked thrush (GCTH, *Catharus minimus*; Lowther et al. 2001; n = 2565), golden-crowned kinglet (GCKI, *Regulus satrapa*; Swanson et al. 2012; n = 7288), hermit thrush (HETH, *Catharus guttatus*; Dellinger et al. 2012; n = 8041), magnolia warbler (MAWA, *Setophaga magnolia*; Hall 1994; n = 10 578), myrtle warbler (MYWA, *Setophaga coronate*; Hunt and Flaspohler 1998; n = 32 473), Nashville warbler (NAWA, *Leiothlypis ruficapilla*; Lowther and Williams 2011; n = 6767), ruby-crowned kinglet (RCKI, *Regulus calendula*; Swanson et al. 2008; n = 12 082), Swainson's thrush (SWTH, *Catharus ustulatus*; Mack and Yong 2000; n = 10 979) and Tennessee warbler (TEWA, *Leiothlypis peregrina*; Rimmer and McFarland 2012; n = 11 900). All of the selected species are migratory, moving from more northern breeding grounds to southerly wintering grounds during the autumn banding period. Although nesting locations and other life history traits vary between species, all are insectivores that breed in forested habitats (<www.allaboutbirds.org>, Cornell Lab of Ornithology).

Banding and data collection

Migrating passerines were captured and banded daily by trained professionals at both sites annually between 1 September and 31 October (Julian date: 244–304) using standard banding protocols (Ralph et al. 2004). The number of nets varied over the years at both locations, ranging from 18 to 35 and 40 to 100 nylon, 12-m, 30-mm mesh nets operated annually at PF and KN, respectively. Nets were opened at sunrise and operated for up to six hours on days when banding occurred. Each net was checked at 40–60 min intervals. The time of capture was recorded as the time when nets were checked. Thus, all birds captured during a particular net check were given the same capture time. A uniquely numbered USGS metal band was affixed to the right leg of each bird for easy identification at recapture and mass was measured to the nearest 0.1 g.

Statistical analysis

Historical weather data was retrieved from Gull Lake Biological Station (42.3941, −85.385), the closest continuously operated weather station. To assess change in temperature over time, daily minimum and daily maximum temperatures were averaged over each autumn (Julian date 244–304) and compared across years (1975–2015) using a general linear model (glm) in program R (Ver. 3.5.2, <www.r-project.org>). Separate analyses were run for daily highs and daily lows (t_{max}, t_{min}; in Celsius), the only temperature variables collected consistently over the duration of the study.

Linear mixed-effect models (lmer, package lme4, Bates et al. 2015) were developed to test for significant temporal trends in: 1) date of arrival, 2) temperature at arrival, 3) capture rate and 4) mass change over the morning hours. Date of arrival (Julian), temperature at arrival (°C) and capture rate (birds/net) models included year, species and the year by species interaction as predictors. Year and location (PF, KN) were also included as random terms in all models. Temperature at arrival was only modeled for maximum daily temperature (t_{max}) because the two temperature terms were highly correlated ($r = 0.747$, $t = 56.20$, $p < 0.001$). Our mass model assessed changes in the rate of mass gain across the morning as years progressed by including the following predictors; year, species, time of day at capture (5:00 a.m. – 12:00 p.m.), year:time, year:species and year:time:species. Time in mass models assessed change at a per minute rate. To present easily interpretable graphics and effect sizes, however, these rates were converted to mass gain over the duration of an entire morning.

For all models, we derived significance using the Anova function (package car, Fox and Weisberg 2011, Table 1). Effect sizes (β) for all terms were derived from model summaries (Supporting information). All models were checked for autocorrelation and normality. Significance for modelled predictors was defined as $p < 0.05$, and determined for species-specific effects by determining whether 95% confidence intervals included zero. Model performance was assessed using conditional R^2, which accounts for variation explained by the combination of fixed and random terms (package MuMin; Nakagawa and Schielzeth 2013).

Results

Daily maximum autumn temperatures (t_{max}) increased significantly from 1975 to 2015 ($\beta = 0.033$, $\chi^2 = 10.28$, $p < 0.001$) with model output indicating that temperature rose by 2.00°C over the 40 year timeframe (Supporting information). However daily minimum temperatures (t_{min}) remained relatively stable ($\beta = 0.006$, $\chi^2 = 0.35$, $p = 0.551$; Supporting information) with model output indicating a 0.28°C change over the same 40 year timeframe.

Date of arrival varied by species ($\chi^2_8 = 21\ 754$, $p < 0.001$) and for the year by species interaction term ($\chi^2_8 = 68\ 518$,

Table 1. Results from linear (weather only) and linear mixed-effects models including banding station location (PF, KN) and year as random terms.

Model	n	R^2	Variable	χ^2	df	p
Weather	40	0.204	Year (t_{max})	10.28	1	0.001
	40	0.009	Year (t_{min})	0.35	1	0.551
Date of arrival (Julian)	102,673	0.781	Year	2.52	1	0.112
			Species	21 754	8	< 0.001
			Year:species	685.18	8	< 0.001
Temperature at arrival (t_{max})	102,673	0.479	Year	34.35	1	< 0.001
			Species	37 148.32	8	< 0.001
			Year:species	18.36	8	0.018
Capture rate	585	0.613	Year	1.45	1	0.228
			Species	735.06	8	< 0.001
			Year:species	15.67	8	0.047
Mass	60,627	0.969	Year	2.56	1	0.109
			Time (of day)	349.03	1	< 0.001
			Species	19 137	8	< 0.001
			Year:time	4.58	1	0.032
			Year:species	238.01	8	< 0.001
			Year:time:species	48.39	8	< 0.001

$p < 0.001$). It did not vary by year as a conditional effect ($\chi^2_1 = 2.52$, $p = 0.112$). Hermit thrushes, ruby-crowned kinglets and myrtle warblers arrived significantly later over time, while Swainson's thrushes, gray-cheeked thrushes and Tennessee warblers arrived significantly earlier over time (Fig. 1). Modelled effect sizes over the 40 year time period ranged from a 4.69 day advance in arrival for the Tennessee warbler, to a 2.02 day delay for the ruby-crowned kinglet. Temperature at arrival (t_{max}) increased significantly by year ($\chi^2_1 = 34.35$, $p < 0.001$), and varied between species ($\chi^2_8 = 37148.32$, $p < 0.001$). Although temperature at arrival increased significantly over time for each species, the pattern of change over time also varied between species ($\chi^2_8 = 279.71$, $p < 0.001$, Fig. 1). In the most extreme case, model output indicated that temperature at arrival for the gray-cheeked thrush rose from 19.96°C in 1975 to 24.77°C by 2015. The myrtle warbler experienced the smallest increase in temperature at arrival (+1.45°C).

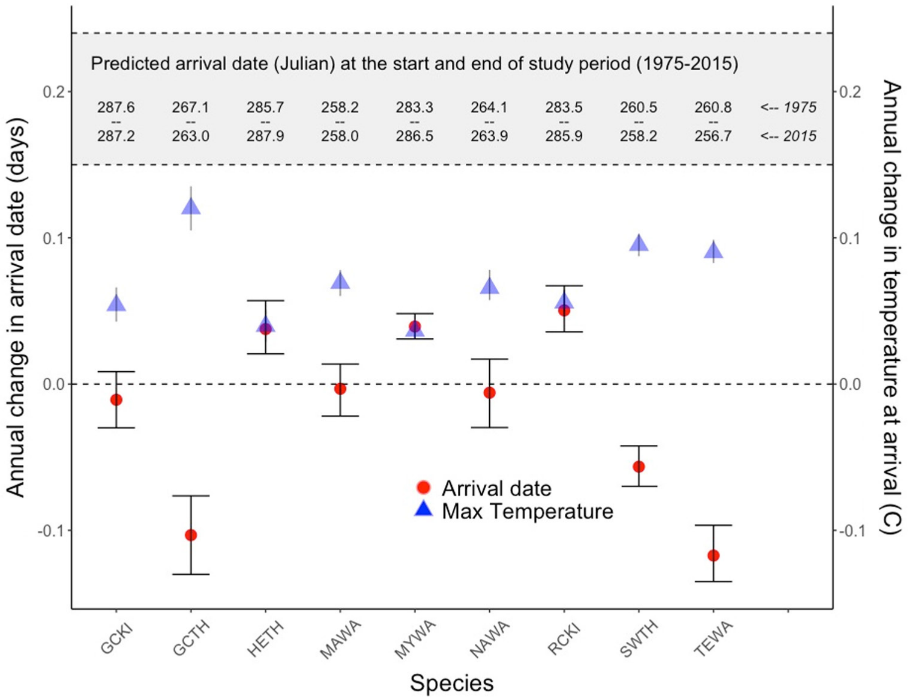

Figure 1. Annual change in mean arrival dates (circle) and maximum (triangle) temperature at arrival. Modelled coefficients for each species are plotted with 95% CI. Species are organized in alphabetical order. Numbers above each species in the gray upper quadrant represent modelled mean arrival date at the beginning (top) and end (bottom) of the study period (i.e. 1975–2015).

Capture rate varied by species ($\chi^2_8=735.06$, $p < 0.001$) and for the interaction between year and species ($\chi^2_8=15.67$, $p=0.048$). It did not vary by year as a conditional effect ($\chi^2_1=1.45$, $p=0.228$). Capture rate increased significantly over time for the hermit thrush, Nashville warbler and ruby-crowned kinglet, and was non-significant in all other species (Supporting information). Patterns in mass gain over the morning differed significantly by species ($\chi^2_8=191327$, $p < 0.001$), time of day ($\chi^2_1=349.03$, $p < 0.001$) and the interactions between year and time ($\chi^2_1=4.58$, $p=0.032$), year and species ($\chi^2_8=238.01$, $p < 0.001$) and year, time and species ($\chi^2_8=48.39$, $p < 0.001$). Only year as a conditional term was not significant ($\chi^2_1=2.56$, $p=0.109$). Of primary interest was the significant 3-way interaction between year, time and species because this result indicated whether patterns of mass gain changed over the years. Mass gain over the morning hours increased significantly over the years in Tennessee, Nashville, myrtle and magnolia warblers, in ruby- and golden-crowned kinglets, and in the hermit thrush (Fig. 2). Mass gain over the morning hours did not vary significant across years in the three remaining species. All species gained mass over the morning period throughout the study (Fig. 2, gray inset).

Discussion

We hypothesized that migratory songbirds would shift their patterns of arrival at stopover sites in western Michigan over time to mitigate the effect of experiencing rising arrival air temperatures. As predicted, the majority of species (six of nine) did exhibit significant shifts in arrival timing. However, temperature at arrival increased significantly over time for all nine species despite delays in arrival dates for three species. Further, three species arrived significantly earlier over time, indicating that stabilizing arrival temperature is either not possible, or of lower priority in these species. Despite the rising arrival temperatures, we found no evidence of reduced station use, or reduction in mass gain over the morning period. Conversely, three of nine species were captured more often over time, and six species gained more mass across the morning period as years progressed. Taken as a whole, our data indicate that the area surrounding our banding sites continues to function as refueling stopovers despite changing climatic conditions and arrival times.

The variable direction of change in arrival dates between species might be related to migratory travel distance. Neotropical migrants are often divided into short- and long-distance migrants (Lincoln 1935), classified based on whether the species primarily remains within North America (short) or travels annually between North and South America (long; Zelt et al. 2017). The ruby-crowned kinglet, golden crowned kinglet, hermit thrush and myrtle warbler fit the short-distance definition, and all but the golden-crowned kinglet significantly delayed their arrival. This pattern of arrival is consistent with other literature on short-term migrants (Saino et al. 2011, Mayor et al. 2017). The five remaining species are characterized as long-distance migrants, and three

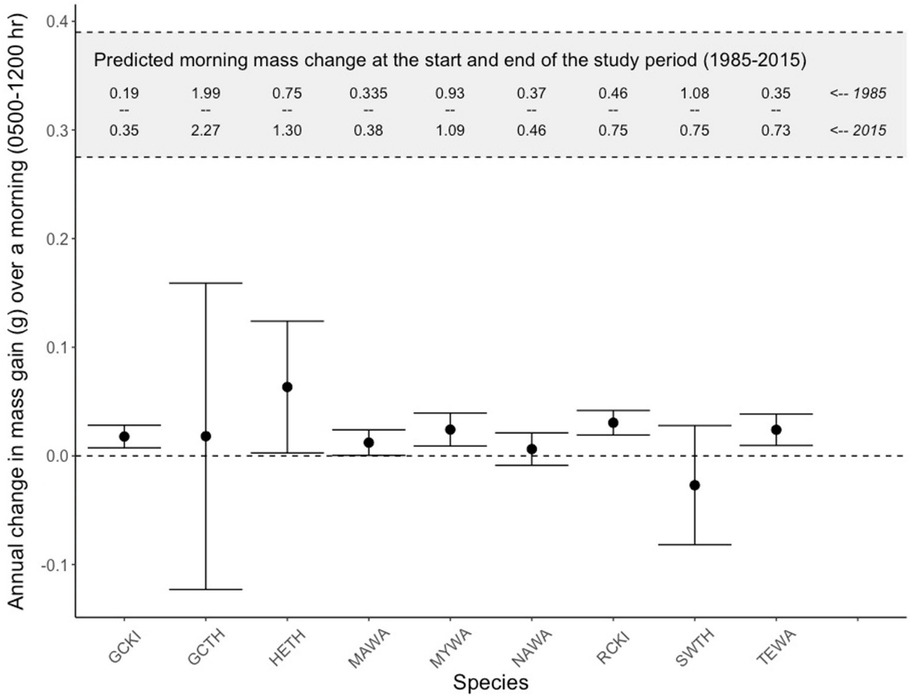

Figure 2. Annual change in mass gain over a morning. Modelled coefficients for each species are plotted with 95% CI. Species are organized in alphabetical order. Numbers above each species label in the gray upper quadrant represent model predicted change in mass over a morning at the beginning (top) and end (bottom) of the study period (i.e. 1985–2015).

of these species (gray-cheeked thrush, Swainson's thrush and Tennessee warbler) advanced their autumn arrival over time. Several studies indicate that long-distance migrants also arrive earlier in the spring (Jenni and Kéry 2003, Jonzén et al 2006). This allows single brooded species, to complete the breeding cycle earlier and potentially facilitates earlier departure from the breeding grounds (Van Buskirk et al. 2009, Gallinat et al. 2015).

Neither delaying nor advancing arrival dates offset increasing arrival temperatures. Perhaps other factors exert more selective pressure on arrival dates, such as temperatures on northern breeding ranges, the movement of air masses and competition on the wintering grounds (Richardson 1978, Kokko 1999, Chambers et al. 2014, Nilsson et al. 2013, Schmaljohann and Both 2017). Notably, all nine species continued to gain mass over morning despite the changes in arrival temperature, and six of them increased the rate of mass gain over time. Rising arrival temperatures may result in a different, but abundant, set of foraging resources (Nooten et al. 2014). For example, a different suite of insect prey may be available earlier, or later, in the season. The same situation may apply to berries and other frugivorous resources, but empirical work is needed to establish this pattern. An alternative hypothesis would be that continued mass gain is mediated by fewer individuals using the site, and thus, its resources. But our results indicate that site use was stable or increasing in all nine study species.

Although insect and floral mismatches due to changing temperatures are of concern (Donnelly et al. 2011, Renner and Zohner 2018), the impacts of temperature change on total abundance of insect populations and biomass of floral production may be of greater issue. Avian migrants may be able to switch prey species under an altered phenology, although reduced food availability could eventually become an insurmountable obstacle. Early research on the impact of temperature on insect populations suggests that continued warming could impact abundance (Cornelissen 2011, Lister and Garcia 2018). Urbanization, invasive species and insecticides also dramatically reduced insect populations (Goulson 2014, Narango et al. 2018, Seress et al. 2018). While our data suggest that western Michigan stopover sites continue to function ecologically, we must be wary of dangerous thresholds associated with continued human activity. Significant warming at our sites indicates that change is already occurring. Measures that minimize or slow the pace of anthropogenic change may be critical for preserving migratory refueling sites in western Michigan and across the world.

Transparent Peer Review

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Data availability statement

Data available from the OSF: <https://osf.io/dq4rz/> (VanTol et al. 2020).

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Author contributions

Schuyler VanTol: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Writing – original draft (lead); Writing – review and editing (supporting). **Carolyn Koehn**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Rich Keith**: Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Brenda Keith**: Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Darren Proppe**: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (lead); Writing – original draft (equal); Writing – review and editing (lead).

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