

Changes in autumn arrival of long-distance migratory birds in Southeast Asia

J. Berton C. Harris^{1,2,*}, Ding Li Yong³, Navjot S. Sodhi^{4,†}, R. Subaraj⁴,
Damien A. Fordham¹, Barry W. Brook¹

¹Environment Institute and School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia 5005, Australia

²Woodrow Wilson School of Public and International Affairs, Princeton University, Princeton, New Jersey 08544, USA

³Nature Society (Singapore), 510 Geylang Road #02-05, The Sunflower, 389466 Singapore

⁴Department of Biological Sciences, National University of Singapore, 117543 Singapore

ABSTRACT: Climate-change-induced phenological changes in migratory birds are predicted from ecological theory and have been well-documented in temperate-zone breeding areas. By contrast, changes in arrival date on tropical wintering grounds have not been reported. To address this gap, we analysed birdwatchers' records of first arrival dates of 9 species of long-distance migratory birds in Singapore from 1987 to 2009. The study species included 1 raptor, 3 waders and 5 passerines. We compared the relative influence of year, Southern Oscillation Index and observer effort on arrival date. There was strong evidence for an arrival delay of approximately 2 d yr⁻¹ (95% confidence intervals of 1–3 d) in Japanese sparrowhawk *Accipiter gularis* and curlew sandpiper *Calidris ferruginea*, but there was no change in arrival date for the other 7 species. We hypothesise that climate change is causing a shift in migration timing for some birds in Southeast Asia. A mechanism for the delay in these long-distance migrants may be that warmer temperatures enable species to remain on northern breeding grounds longer. Delayed arrival on the wintering grounds may have cascading effects on a migratory species' annual cycle, for example by influencing the arrival date at the breeding grounds, which can impact fitness. These potential impacts underscore the need for further work on the effects of climate change on migratory species in the tropics.

KEY WORDS: *Accipiter gularis* · *Calidris ferruginea* · Citizen science · Climate change · Migration · Phenology

—Resale or republication not permitted without written consent of the publisher—

1. INTRODUCTION

Changes in phenology are among the best-documented and most consistently observed impacts of climate change on animals (Lehikoinen & Sparks 2010). For migratory birds, it is well established that spring arrival dates on the European and North American breeding grounds are advancing (reviewed by Lehikoinen & Sparks 2010, Knudsen et al. 2011), but responses are expected to vary regionally (Askeyev et al. 2010). Long-distance migrants are often thought to have endogenous control of migration timing because they are unaware of weather conditions

where they are headed (Gwinner 1996), while short-distance migrants may be more flexible in their capacity to alter migration timing based on their perception of regional weather conditions, especially if they migrate slowly (Hötker 2002, Hurlbert & Liang 2012). Nonetheless, a recent review found no consistent differences in spring arrival changes between short- and long-distance migrants (Knudsen et al. 2011).

Autumn departure and passage are less studied than spring arrival, and there is much variation in changes in autumn departure and passage over time, with no clear trend of advances or delays (Thorup et

*Email: johnbh@princeton.edu

†Deceased

al. 2007, Lehtikoinen & Sparks 2010). Several north-temperate studies found that long-distance passerines have advanced their autumn departure (Cotton 2003, Jenni & Kéry 2003, Péron et al. 2007, Van Buskirk et al. 2009), while short-distance migrants have delayed departure (Jenni & Kéry 2003, Van Buskirk et al. 2009). Advances of long-distance migrants could be related to advances in the overall annual cycle associated with earlier spring arrival (Gilyazov & Sparks 2002, Lehtikoinen et al. 2004, Lehtikoinen & Sparks 2010; but see Thorup et al. 2007, Van Buskirk et al. 2009). Other north-temperate passerine studies have found general delays in autumn passage in short- (Smith & Paton 2011) and long-distance migrants (Kovács et al. 2011, 2012, Smith & Paton 2011), while still others have found more variation. For example, Tøttrup et al. (2006) found that migration distance was inversely proportional to earlier autumn departure in European passerines, and Mills (2005) studied passerines in Ontario, Canada, and found that 1 long-distance and 4 short-distance migrants delayed passage, while 2 long-distance species advanced it. In one of the most comprehensive multi-species studies, Sparks et al. (2007) found significantly delayed autumn departure in 15 species in 20 out of 67 time series that were at least 20 yr long.

The little research done on non-passerine autumn passage has also indicated variable changes. In studies of long-distance migrant waders in Central Europe, Adamík & Pietruszkova (2008) found that 3 species advanced and 3 delayed autumn passage, and Anthes (2004) found 3 species delayed autumn passage. Filippi-Codaccioni et al. (2010) found that 1 short-distance and 4 long-distance raptors advanced autumn passage, while Van Buskirk (2012) recorded autumn delays in 10 species and an advance in 1 species. The above variation in autumn passage is likely related to differing mechanisms behind changes among species (especially relating to life-history traits) and regions, but more research is required to better understand these patterns on a species-specific basis (Rubolini et al. 2007, Møller et al. 2008, Lehtikoinen & Sparks 2010, Végvári et al. 2010).

Even less is known of how changes in autumn departure and passage in the northern hemisphere translate into changes in arrival on the wintering grounds. Studies with light-sensing geolocators have revealed that migrant departure date is correlated with arrival date on the wintering grounds, but individual birds vary in their rate of migration and time spent at stopover sites, so departure date is only a partial predictor of wintering grounds arrival date

(Stutchbury et al. 2011, Stanley et al. 2012). The few southern hemisphere analyses that have measured changes in time of arrival at wintering grounds found advances in 3 Siberian breeders in south-eastern Australia (Beaumont et al. 2006) and in 8 short-distance migrants in southern Australia (Chambers 2005, Smith & Smith 2012), but no significant changes in timing of arrival for the long-distance migratory barn swallow *Hirundo rustica* in South Africa (Altwegg et al. 2012). In addition, Kok et al. (1991) presented first arrival dates for spotted flycatchers *Muscicapa striata* on their South African wintering grounds from 1950 to 1986, and it appears that arrival occurred later over time (J. B. C. Harris pers. obs.), but this observation was not tested by the authors.

Changes in arrival date on the tropical wintering grounds and passage through the tropics are unstudied, probably because of the paucity of long-term tropical datasets (Gordo 2007, Lehtikoinen & Sparks 2010). Yet, analyses from the tropics are urgently needed because hundreds of species make temperate-tropical journeys, and changes in timing can impact other stages in the annual cycle (Marra et al. 1998). For example, late arrival on the wintering grounds may have negative consequences if species compete for non-breeding territories (Faaborg et al. 2010), and birds that occupy poor wintering territories have been shown to arrive later on the breeding grounds which could force them into lower-quality territories, or to expend energy competing with earlier arrivals (Norris et al. 2004).

We studied changes in first arrival date of 9 long-distance migrants, comprising passerines (Passeriformes), waders (Charadriiformes) and a raptor (Falconiformes), from 1987 to 2009 in Singapore, a natural bottleneck in the East Asian flyway with diverse habitats and a long history of birdwatching. Our study examined common, generalist species to evaluate whether any changes in migration timing were evident. Given that much of East Asia has warmed by $>0.2^{\circ}\text{C}$ per decade since the 1960s (Solomon et al. 2007), and that migration timing has been linked to temperature (Lehtikoinen & Sparks 2010), we hypothesised that some of our study species would change their migration phenology.

2. METHODS

First arrival dates came from birdwatchers' records that were verified by local experts and published monthly in the Singapore Bird Group's newsletter 'Singapore Avifauna' (Lim & Subaraj 1987–1990, 1992,

1997, 1998, 2000–2003, 2006, 2008, 2009). The ‘Singapore Avifauna’ data came from reports by skilled recreational birdwatchers. More birdwatchers tended to go into the field during migration and on weekends; approximately 5 to 30 observers went out each week during autumn passage from July to December (our study period). Difficult-to-detect species may require more time to be found, such as is available to birdwatchers on weekends, which can lead to biased reports of species occurrence—the ‘weekend effect’ (Sparks et al. 2007, 2008); our focus on common, easily detectable species (see below) should minimize this potential bias (Ptaszyk et al. 2003, Sparks et al. 2008). All Singaporean sites known to host substantial numbers of migrants were visited by birdwatchers annually.

Full arrival distribution data are preferable to first arrival dates because the latter are an incomplete sample of the population (Sparks et al. 2001, Tryjanowski et al. 2005, Miller-Rushing et al. 2008, Van Buskirk et al. 2009, Lehikoinen & Sparks 2010), but first arrival dates are often the only data available, especially from poorly studied regions (Lehikoinen et al. 2004, Beaumont et al. 2006, Gordo & Doi 2012). Compared to mean arrival dates, first arrival dates often suggest stronger shifts in migration timing that may be more variable geographically, but the sign of change is usually in the same direction as mean arrival dates (Rubolini et al. 2007, Thorup et al. 2007, Lehikoinen & Sparks 2010).

Singapore was originally covered in lowland rainforest with mangroves and tidal flats on the coast. Over the past 200 yr, most forests were replaced with cropland and then urban development, while many coastal wetlands were filled in for urban and shipping development (Hails 1989, Corlett 1992). These changes caused extinctions of forest-dependent species, but the country still has a resident avifauna of 146 breeding species and is an important stopover and wintering site for migratory land and water birds, with at least 115 additional species recorded annually (Wells 1999, 2007, Brook et al. 2003, Lim 2009, Lim & Lim 2009).

Our study species are common birds that were seen each year, and habitat generalists that should be weakly affected by deforestation (Lim & Lim 2009, Wells 1999, 2007). Habitat preferences of migratory birds on the Asian wintering grounds are poorly known, but all of our passerine and raptor study species are able to use a range of habitats and, for most, interior forest is probably not preferred (e.g. tiger shrike *Lanius tigrinus*; arctic warbler *Phylloscopus borealis*; Wells 2007). There have been no water bird

extirpations in Singapore, despite historic wetland conversion (Lim & Lim 2009). Most of Singapore’s wetland loss occurred before our study period (Hails 1989, Lim 2009). The small reduction in wetland habitat observed during our study period would not be expected to affect the arrival dates of waders because large areas of mudflats and wet grasslands still exist at sites such as Sungei Buloh, Mandai wetlands, Pulau Ubin, Changi North-Central, Jurong West and Punggol, and these same focal sites were visited by observers each year (Lim 2009, Lim & Lim 2009). Highly skilled observers submitted observations to ‘Singapore Avifauna’ annually, so it is unlikely that changes in identification ability affected arrival dates (R. Subaraj pers. obs.).

Birdwatching effort and reporting in Singapore have varied over time (Wee 2006), which could potentially confound our analysis. We accounted for this in the following ways. Firstly, Singapore bird experts among the co-authors (D.L.Y. and R.S.) removed records of post-breeding dispersal and very late ‘first arrival’ records (seen after migration) that were due to incomplete sampling. Our study species are common migrants, and all study species were seen each year (i.e. changes in population size had no effect on whether a species was recorded that year). Secondly, observer effort in each year was characterised, and only well-sampled years were analysed. We evaluated sampling coverage on an initial pool of 36 potential study species that had at least 8 years with reliable arrival dates (i.e. seen during migration). We made the *a priori* rule that a year was considered to be adequately sampled when a reliable arrival date was recorded for >15 of the 36 species, leaving 14 years from the 1987–2009 span for the analysis. We defined observer effort as the proportion of 36 bird species for which a reliable arrival date was available that year (Fig. 1). This measure of observer effort was added as a predictor variable to the candidate model set (see this section below). As a final step, we chose to analyse only those species in the pool of 36 potential species with the best data (i.e. having time series of at least 13 years), which left 9 study species. Japanese sparrowhawk *Accipiter gularis*, common sandpiper *Actitis hypoleucos*, tiger shrike and Siberian blue robin *Luscinia cyane* had time series of 13 years; the remaining species had series of 14 years. All of our study species breed north of ca. 25° N, so we considered them to be long-distance migrants.

Changes in population size can influence detection probability (Tryjanowski & Sparks 2001), and abundance may also respond to climate change (Sokolov

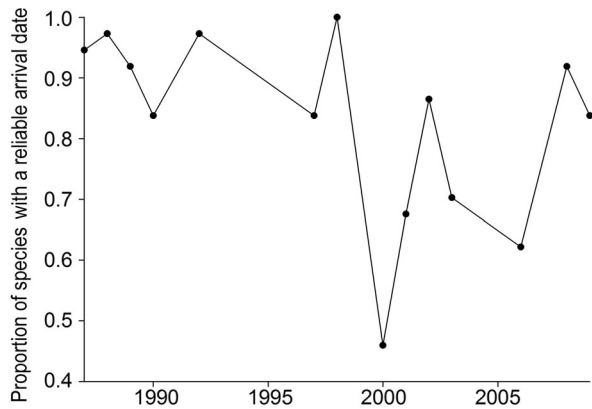


Fig. 1. Observer effort during the study, measured by the proportion of 36 bird species for which a reliable arrival date was available that year. The 36 species are migratory birds that we considered in the initial pool of possible species for the current study. We used the larger pool of species to evaluate observer effort, but used the 9 species with the longest time series for the final arrival date analysis. In years of lower observer effort fewer species were observed during migration, but all 36 species were observed annually

et al. 2000), so we characterised population trends for our study species. Few high-quality local- or regional-scale population trend data were available, so we used global measures of population status for most species (BirdLife International 2011). Global trend information was unavailable for purple-backed starling *Agropsar sturninus*, so we approximated status for this species based on Singapore trend data provided by Lim & Lim (2009). In contrast to information from BirdLife International (2011), data from the Asian-Australasian flyway indicate that curlew sandpiper *Calidris ferruginea* is declining (Bamford et al. 2008). The literature indicated that Japanese sparrowhawk, arctic warbler, yellow-rumped flycatcher *Ficedula zanthopygia* and purple-backed starling are stable, and curlew sandpiper, ruddy turnstone *Arenaria interpres*, common sandpiper, tiger shrike and Siberian blue robin are declining. None of the study species is considered by the IUCN to be threatened (BirdLife International 2011).

The large range of latitudes where our study species breed (ca. 25–80°N) made it unfeasible to include local temperature as a predictor of arrival date. Instead, we opted to use the Southern Oscillation Index (SOI; Bureau of Meteorology 2011) as a measure of El Niño-related changes in regional climate. El Niño/Southern Oscillation has been shown to have profound effects on climate in the Asia-Pacific region (e.g. Wang et al. 2001) and has correlated with changes in avian migration timing in other studies (Lehikoinen & Sparks 2010).

Gaussian general linear models were used to compare the importance of year, SOI and observer effort on arrival date using a maximum-likelihood, multi-model inference framework, implemented in R v2.14.1 (Burnham & Anderson 2002, R Development Core Team 2012). Arrival date (day of year) was the response variable in our analyses. We ran separate analyses for each species. For the species with 14 years of arrival dates, we used all additive combinations of predictor variables. In species with 13 years of arrival dates, we did not include the global model (Arrival Date \approx Year + Observer Effort + SOI) to avoid over-fitting (Burnham & Anderson 2002), because this model's number of parameters (5) is greater than 30% of the sample size. Constrained sample sizes did not permit testing the effects of population trend. We tested for correlations among predictors with a Spearman correlation matrix and found that all variables had Spearman coefficients < 0.55 . We checked diagnostic plots of the relationship between the fitted values and residuals, the quantiles in the data against theoretical normal quantiles and the relationship between leverage and standardised residuals to evaluate whether the models met the assumptions of Gaussian regression (Crawley 2007). Bootstrapping (10 000 samples with replacement) was used to generate confidence intervals around slope estimates for the Arrival Date:Year relationship in all species (Crawley 2007). For species with evidence for changed arrival date over time, we calculated model-averaged coefficients of the Arrival Date:Year relationship based on the corrected Akaike's information criterion weights ($wAIC_c$). We used Burnham & Anderson's (2002, p. 152) first model averaging method where the coefficient (Year) is averaged only over models in which it appears, after weights have been rescaled to sum to unity.

3. RESULTS

Two species, Japanese sparrowhawk and curlew sandpiper, showed a delayed arrival date during the study period (Tables 1 & 2, Fig. 2). The single-variable Year model was top ranked for the sparrowhawk and sandpiper, with $wAIC_c$ of 0.58 and 0.46, respectively. The sum of $wAIC_c$ for models including Year as a predictor were 0.982 and 0.993 for the sparrowhawk and sandpiper, respectively. Based on the single-variable Year model, the effect size was similar between the 2 species, a delay of 2.0 d yr⁻¹ (1.1–2.9, 95% confidence interval) for the sparrow-

Table 1. Gaussian general linear model results for arrival date of the 9 study species. % DE: % deviance explained by the model. ΔAIC_c : difference between the model Akaike's information criterion corrected for small sample sizes (AIC_c) and the minimum AIC_c in the set of models; $wAIC_c$: AIC_c weights showing the relative likelihood of the current model; evidence ratio: $W_{top\ model}/W_{current}$, a value of 5 indicates that the top-ranked model is 5 times better supported by the data than the current model. k : number of parameters. Model parameters—Yr: year, Obs: observer effort, SOI: Southern Oscillation Index

Model	% DE	ΔAIC_c	$wAIC_c$	Evidence ratio	k	Model	% DE	ΔAIC_c	$wAIC_c$	Evidence ratio	k
Japanese sparrowhawk <i>Accipiter gularis</i>						Tiger shrike <i>Lanius tigrinus</i> (continued)					
Yr	67.4	0	0.58		3	Yr + Obs	25.9	3.9	0.068	7.0	4
Yr + SOI	74.1	1.4	0.291	2.0	4	Obs + SOI	14.9	5.7	0.028	17.2	4
Yr + Obs	69.9	3.3	0.111	5.2	4	Yr + SOI	3.8	7.3	0.012	38.3	4
Obs + SOI	56.3	8.2	0.01	59.0	4	Arctic warbler <i>Phylloscopus borealis</i>					
Obs	32.0	9.6	0.005	120.0	3	Null	0	0	0.441		2
Null	0	11.1	0.002	260.1	2	Obs	12.5	1.4	0.214	2.1	3
SOI	7.2	13.6	0.001	906.4	3	SOI	7.4	2.2	0.144	3.1	3
Common sandpiper <i>Actitis hypoleucos</i>						Yr	3.2	2.9	0.106	4.2	3
Null	0	0	0.494		2	Obs + SOI	16.5	4.8	0.039	11.2	4
Obs	13.8	1.5	0.23	2.2	3	Yr + Obs	12.5	5.5	0.028	15.5	4
SOI	1.7	3.2	0.098	5.1	3	Yr + SOI	10.7	5.8	0.025	17.9	4
Yr	0.8	3.4	0.092	5.4	3	Yr + Obs + SOI	16.7	9.8	0.003	137.5	5
Yr + Obs	21.4	4.7	0.048	10.3	4	Purple-backed starling <i>Agropsar sturninus</i>					
Obs + SOI	14.1	5.8	0.027	18.5	4	Null	0	0	0.436		2
Yr + SOI	2.5	7.5	0.012	42.0	4	Obs	8.9	2.0	0.16	2.7	3
Ruddy turnstone <i>Arenaria interpres</i>						SOI	6.8	2.3	0.136	3.2	3
Null	0	0	0.316		2	Yr	3.6	2.8	0.108	4.0	3
Obs	21.0	0.01	0.314	1.0	3	Yr + Obs	21.8	3.9	0.062	7.0	4
Yr + Obs	32.3	1.9	0.123	2.6	4	Obs + SOI	20	4.2	0.052	8.3	4
Obs + SOI	27.5	2.9	0.076	4.2	4	Yr + SOI	10.6	5.8	0.024	18.0	4
SOI	2.3	3.0	0.071	4.5	3	Yr + Obs + SOI	36.5	6.1	0.021	20.7	5
Yr	1.0	3.2	0.065	4.9	3	Siberian blue robin <i>Luscinia cyane</i>					
Yr + Obs + SOI	41.4	4.9	0.027	11.8	5	Obs	47.8	0	0.564		3
Yr + SOI	3.3	6.9	0.01	31.3	4	Yr + Obs	58.0	1.5	0.266	2.1	4
Curlew sandpiper <i>Calidris ferruginea</i>						Obs + SOI	50.2	3.7	0.088	6.4	4
Yr	58.3	0	0.46		3	Null	0	5.0	0.047	12.0	2
Yr + Obs	68.4	0.2	0.422	1.1	4	SOI	14.8	6.4	0.023	24.1	3
Yr + SOI	58.5	4.0	0.063	7.3	4	Yr	0.8	8.3	0.009	64.5	3
Yr + Obs + SOI	69.9	4.5	0.048	9.6	5	Yr + SOI	15.7	10.6	0.003	195.9	4
Null	0	8.9	0.005	86.9	2	Yellow-rumped flycatcher <i>Ficedula zanthopygia</i>					
Obs	0.3	12.2	0.001	445.7	3	Null	0	0	0.405		2
SOI	0.1	12.2	0.001	451.8	3	Yr	18.4	0.5	0.322	1.3	3
Obs + SOI	0.3	16.2	0	3354.1	4	Obs	2.6	2.9	0.093	4.4	3
Tiger shrike <i>Lanius tigrinus</i>						SOI	0.1	3.3	0.078	5.2	3
Null	0	0	0.478		2	Yr + Obs	18.5	4.5	0.043	9.4	4
Obs	13.9	1.5	0.223	2.1	3	Yr + SOI	18.5	4.5	0.043	9.4	4
Yr	3.4	3.0	0.106	4.5	3	Obs + SOI	3.1	6.9	0.013	31.7	4
SOI	0.2	3.4	0.086	5.6	3	Yr + Obs + SOI	18.6	9.5	0.003	117.4	5

hawk, and a delay of 1.8 d yr^{-1} (0.9–2.5) for the sandpiper. The model-averaged estimate for the Year coefficient was 1.9 d yr^{-1} for both species.

By contrast, the other species showed no change in arrival date over time (Tables 1 & 2). The null model was top-ranked in all of these species except for Siberian blue robin, where Observer Effort was the top model. SOI as a single variable was not a

statistically supported predictor of arrival date for any of the study species. Despite the even split of species (5 stable, including Japanese sparrowhawk, and 4 declining, including curlew sandpiper), there was no clear pattern of changed arrival date based on population trend. Model diagnostics showed that the data met the necessary assumptions for Gaussian-identity link models.

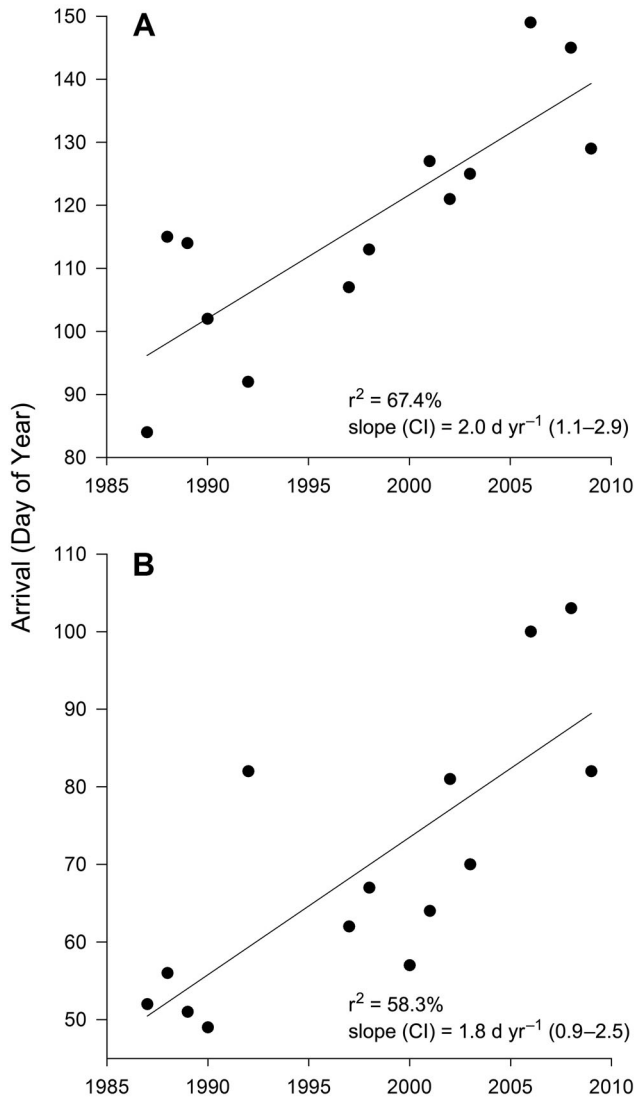


Fig. 2. *Accipiter gularis* and *Calidris ferruginea*. Change in arrival date anomaly over time for (A) Japanese sparrowhawk and (B) curlew sandpiper in Singapore. The 95% confidence intervals are from the percentiles of 10 000 bootstrapped resamples

4. DISCUSSION

Our results indicate that 2 long-distance migrants, Japanese sparrowhawk and curlew sandpiper, have delayed autumn arrival in Singapore. We hypothesise that these changes are related to warming temperatures because the region has warmed considerably during the study period (Solomon et al. 2007), the study species are common generalists that should not be strongly affected by habitat loss in Singapore, and we tested for the effects of changing observer effort. Nonetheless, our findings should be interpreted with caution because first arrival date studies

Table 2. Slope of relationship between year and arrival date for our 9 study species (d yr^{-1} ; ranked by slope). Confidence intervals (CI) are based on the percentiles of 10 000 bootstrapped resamples. **Bold:** evidence for change in arrival date over time (year model top-ranked). *Slope CI does not include 0

Species	Slope (95% CI)
Japanese sparrowhawk	1.96 (1.1 to 2.9)*
Curlew sandpiper	1.77 (0.89 to 2.5)*
Arctic warbler	0.35 (−0.75 to 1.8)
Ruddy turnstone	0.25 (−1.3 to 1.4)
Siberian blue robin	0.15 (−0.89 to 1.1)
Common sandpiper	−0.09 (−0.63 to 0.5)
Purple-backed starling	−0.35 (−0.99 to 0.79)
Tiger shrike	−0.38 (−1.6 to 0.46)
Yellow-rumped flycatcher	−0.97 (−2.0 to 0.25)

do not give information on population-wide changes, and can show stronger (although often concordant) trends compared to full arrival distribution studies (e.g. Mills 2005, Rubolini et al. 2007, Thorup et al. 2007). This pattern of stranger trends in first-arrival-date studies could explain why the slopes of our Arrival Date:Year relationship are larger than slopes reported in most migration phenology studies (Lehikoinen & Sparks 2010). In addition, it is possible that the delay observed in curlew sandpiper arrival could be partially explained by reduced detectability resulting from its declining population (Tryjanowski & Sparks 2001). Nonetheless, we find this explanation unlikely because the species is still recorded in large numbers; for example, at least 200 individuals were recorded annually in a single wetland, Sungei Buloh, in recent years (Gan et al. 2012).

In general, the arrival delays we observed agree with studies showing delayed autumn passage of long-distance migrants (Anthes 2004, Adamík & Pietruszkova 2008, Kovács et al. 2011, 2012, Smith & Paton 2011), but as described in the 'Introduction', there is much variation among species and sites (Cotton 2003, Jenni & Kéry 2003, Péron et al. 2007, Sparks et al. 2007, Van Buskirk et al. 2009). Interestingly, Beaumont et al. (2006) found advances in winter arrival for some long-distance species in Australia, including curlew sandpiper, which showed a strong delay in our study. A substantial proportion of the East Asian population of curlew sandpiper winters in southern Australia (Bamford et al. 2008). It is unclear whether we studied the same populations of this species, but these apparently contradictory results could reflect changes in the rate of migration between sampling sites (sensu Stutchbury et al. 2011, Stanley et al. 2012).

The arrival delays in long-distance migrants could be related to warming temperatures enabling species to remain in northern breeding or passage areas later in the year (Anthes 2004, Lehtikoinen et al. 2004). While the possible mechanism for this pattern is unknown, warmer temperatures could lengthen the growing season when terrestrial or marine prey would be active, or decrease the energetic cost of birds remaining in northern latitudes (Zwarts 1990, Bradshaw & Holzapfel 2006). Japanese sparrowhawk has a markedly different diet, habitat preference and migration strategy compared to curlew sandpiper (e.g. *Accipiter* migration is not confined to the coast, and waders tend to migrate at night; Richardson 1979), which suggests that different mechanisms could underlie the delays we observed. It is unclear why the other species in our study did not change their migration timing, but this lack of response is consistent with the mixed results (including no changes) shown in autumn departure and passage studies (Mills 2005, Thorup et al. 2007, Van Buskirk et al. 2009).

Changes in arrival timing have conservation implications for species, and potentially, ecosystems. Delayed arrival on the wintering grounds may affect territory acquisition, which can be related to arrival timing on the breeding grounds and, eventually, fitness (Marra et al. 1998). Furthermore, mis-timing can result when species change their phenology at different rates. For example, populations of pied flycatcher *Ficedula hypoleuca* that arrive after the peak emergence of their primary food source are prone to decline (Both et al. 2006). Wader prey abundance can also be related to temperature (Zwarts 1990), which could cause similar mistiming.

In conclusion, we conducted the first analysis of changes in avian migratory phenology in the tropics. We found evidence for arrival delays in Japanese sparrowhawk and curlew sandpiper, but no changes in our other study species. During our study period the climate warmed across Asia (Solomon et al. 2007), which suggests that the observed changes may be related to warming temperatures. The effects of changes in migration timing on migratory species' annual cycles emphasise the need for further analyses on climate change impacts on migratory species in the tropics.

Acknowledgements. We are grateful to G. Maurer for comments on wader population trends, and P. Cassey, S. Delean, S. de Little and S. Gregory for statistical advice. Three anonymous reviewers provided valuable comments on the manuscript. J.B.C.H. was funded by the Loke Wan Tho Memorial Foundation and an EIPR scholarship at the University of Adelaide.

LITERATURE CITED

- Adamík P, Pietruszkova J (2008) Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithol* 43:119–128
- Altwegg R, Broms K, Erni B, Barnard P, Midgley GF, Underhill LG (2012) Novel methods reveal shifts in migration phenology of barn swallows in South Africa. *Proc R Soc Lond B Biol Sci* 279:1485–1490
- Anthes N (2004) Long-distance migration timing of *Tringa* sandpipers adjusted to recent climate change. *Bird Study* 51:203–211
- Askeyev O, Sparks T, Askeyev I, Tishin D, Tryjanowski P (2010) East versus West: contrasts in phenological patterns? *Glob Ecol Biogeogr* 19:783–793
- Bamford M, Watkins D, Bancroft W, Tischler G, Wahl J (2008) Migratory shorebirds of the east Asian-Australasian flyway: population estimates and internationally important sites. Wetlands International-Oceania, Canberra
- Beaumont LJ, McAllan IAW, Hughes L (2006) A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Glob Change Biol* 12:1339–1354
- BirdLife International (2011) BirdLife International data zone. Available at www.birdlife.org/datazone/home (accessed 5 September 2011)
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83
- Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science* 312:1477–1478
- Brook BW, Sodhi NS, Ng PKL (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature* 424:420–426
- Bureau of Meteorology (2011) Southern Oscillation Index archives. Bureau of Meteorology, Australian government. Available at www.bom.gov.au/climate/current/soi2.shtml (accessed 1 November 2011)
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference, 2nd edn. Springer, New York, NY
- Chambers LE (2005) Migration dates at Eyre Bird Observatory: links with climate change? *Clim Res* 29:157–165
- Corlett RT (1992) The ecological transformation of Singapore, 1819–1990. *J Biogeogr* 19:411–420
- Cotton PA (2003) Avian migration phenology and global climate change. *Proc Natl Acad Sci USA* 100:12219–12222
- Crawley MJ (2007) The R book. Wiley, Chichester
- Faaborg J, Holmes RT, Anders AD, Bildstein KL and others (2010) Recent advances in understanding migration systems of New World land birds. *Ecol Monogr* 80:3–48
- Filippi-Codaccioni O, Moussus JP, Urcun JP, Jiguet F (2010) Advanced departure dates in long-distance migratory raptors. *J Ornithol* 151:687–694
- Gan J, Tan M, Li D (2012) Migratory birds of Sungei Buloh Wetland Reserve, 2nd edn. National Parks Board, Singapore
- Gilyazov A, Sparks T (2002) Change in the timing of migration of common birds at the Lapland Nature Reserve (Kola Peninsula, Russia) during 1931–1999. *Avian Ecol Behav* 8:35–47
- Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58
- Gordo O, Doi H (2012) Drivers of population variability in

- phenological responses to climate change in Japanese birds. *Clim Res* 54:95–112
- Gwinner E (1996) Circannual clocks in avian reproduction and migration. *Ibis* 138:47–63
- Hails CJ (1989) Singapore. In: Scott DA (ed) A directory of Asian wetlands. IUCN wetland directories. IUCN, Gland. Available at <http://ramsar.wetlands.org/Portals/15/Singapore.pdf>
- Hötter H (2002) Arrival of pied avocets *Recurvirostra avosetta* at the breeding site: effects of winter quarters and consequences for reproductive success. *Ardea* 90:379–387
- Hurlbert AH, Liang Z (2012) Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PLoS ONE* 7:e31662
- Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc R Soc Lond B Biol Sci* 270:1467–1471
- Knudsen E, Lindén A, Both C, Jonzén N and others (2011) Challenging claims in the study of migratory birds and climate change. *Biol Rev Camb Philos Soc* 86:928–946
- Kok OB, Van Ee CA, Nel DG (1991) Daylength determines departure date of the spotted flycatcher *Muscicapa striata* from its winter quarters. *Ardea* 79:63–66
- Kovács S, Csörg T, Harnos A, Fehérvári P, Nagy K (2011) Change in migration phenology and biometrics of two conspecific *Sylvia* species in Hungary. *J Ornithol* 152:365–373
- Kovács S, Fehérvári P, Nagy K, Harnos A, Csörg T (2012) Changes in migration phenology and biometrical traits of reed, marsh and sedge warblers. *Cent Eur J Biol* 7:115–125
- Lehikoinen E, Sparks T (2010) Changes in migration. In: Møller AP, Fiedler W, Berthold P (eds) Effects of climate change on birds. Oxford University Press, Oxford, p 89–112
- Lehikoinen E, Sparks T, Zalakevicius M (2004) Arrival and departure dates. *Adv Ecol Res* 35:1–31
- Lim KC, Lim KS (2009) State of Singapore's wild birds and bird habitats. A review of the annual bird census 1996–2005. Nature Society (Singapore), Singapore
- Lim KS (2009) The avifauna of Singapore. Nature Society (Singapore), Singapore
- Lim KS, Subaraj R (1987–1990, 1992, 1997, 1998, 2000–2003, 2006, 2008, 2009) Bird reports, July–December. Singapore Avifauna 1–4, 6, 11–12, 14–16, 19, 21–22
- Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886
- Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzinger P (2008) Bird migration times, climate change, and changing population sizes. *Glob Change Biol* 14:1959–1972
- Mills AM (2005) Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* 147:259–269
- Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc Natl Acad Sci USA* 105:16195–16200
- Norris DR, Marra PP, Montgomerie R, Kyser TK, Ratcliffe LM (2004) Reproductive effort, molting latitude, and feather color in a migratory songbird. *Science* 306:2249–2250
- Péron G, Henry PY, Provost P, Dehorter O, Julliard R (2007) Climate changes and post-nuptial migration strategy by two reedbed passerines. *Clim Res* 35:147–157
- Ptaszyk J, Kosicki J, Sparks T, Tryjanowski P (2003) Changes in the timing and pattern of arrival of the white stork (*Ciconia ciconia*) in western Poland. *J Ornithol* 144:323–329
- R Development Core Team (2012) R: a language and environment for statistical computing. Version 2.14.1. R Foundation for Statistical Computing, Vienna. Available at www.R-project.org
- Richardson WJ (1979) Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. *Can J Zool* 57:107–124
- Rubolini D, Møller AP, Rainio K, Lehikoinen E (2007) Intra-specific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Clim Res* 35:135–146
- Smith P, Smith J (2012) Climate change and bird migration in south-eastern Australia. *Emu* 112:333–342
- Smith SB, Paton PWC (2011) Long-term shifts in autumn migration by songbirds at a coastal eastern North American stopover site. *Wilson J Ornithol* 123:557–566
- Sokolov LV, Yefremov VD, Markovets MY, Shapoval AP, Shumakov ME (2000) Monitoring of numbers in passage populations of passerines over 42 years (1958–1999) on the Courish Spit of the Baltic Sea. *Avian Ecol Behav* 4:31–53
- Solomon S, Qin D, Manning M, Chen Z and others (eds) (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Sparks TH, Roberts DR, Crick HQP (2001) What is the value of first arrival dates of spring migrants in phenology? *Avian Ecol Behav* 7:75–85
- Sparks TH, Huber K, Bland RL, Crick HQP and others (2007) How consistent are trends in arrival (and departure) dates of migrant birds in the UK? *J Ornithol* 148:503–511
- Sparks TH, Huber K, Tryjanowski P (2008) Something for the weekend? Examining the bias in avian phenological recording. *Int J Biometeorol* 52:505–510
- Stanley CQ, MacPherson M, Fraser KC, McKinnon EA, Stutchbury BJM (2012) Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE* 7:e40688
- Stutchbury BJM, Gow EA, Done T, MacPherson M, Fox JW, Afanasyev V (2011) Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proc R Soc Lond B Biol Sci* 278:131–137
- Thorup K, Tøttrup A, Rahbek C (2007) Patterns of phenological changes in migratory birds. *Oecologia* 151:697–703
- Tøttrup AP, Thorup K, Rahbek C (2006) Changes in timing of autumn migration in North European songbird populations. *Ardea* 94:527–536
- Tryjanowski P, Sparks TH (2001) Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. *Int J Biometeorol* 45:217–219
- Tryjanowski P, Kuźniak S, Sparks TH (2005) What affects the magnitude of change in first arrival dates of migrant birds? *J Ornithol* 146:200–205
- Van Buskirk J (2012) Changes in the annual cycle of North American raptors associated with recent shifts in migration timing. *Auk* 129:691–698
- Van Buskirk J, Mulvihill RS, Leberman RC (2009) Variable shifts in spring and autumn migration phenology in

- North American songbirds associated with climate change. *Glob Change Biol* 15:760–771
- Végyvári Z, Bókony V, Barta Z, Kovács G (2010) Life history predicts advancement of avian spring migration in response to climate change. *Glob Change Biol* 16:1–11
- Wang Y, Wang B, Oh JH (2001) Impact of the preceding El Niño on the East Asian summer atmosphere circulation. *J Meteorol Soc Japan* 79:575–588
- Wee YC (2006) Forty years of birding and ornithological research in Singapore. *Birding Asia* 5:12–15
- Wells DR (1999) *The birds of the Thai-Malay peninsula*, Vol 1. Non-passerines. Academic Press, San Diego, CA
- Wells DR (2007) *The birds of the Thai-Malay peninsula*, Vol 2. Passerines. Christopher Helm, London
- Zwarts L (1990) Increased prey availability drives pre-migration hyperphagia in whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time. *Ardea* 78:279–300

*Editorial responsibility: Tim Sparks,
Cambridge, UK*

*Submitted: November 23, 2012; Accepted: June 16, 2013
Proofs received from author(s): August 5, 2013*