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Autumn phenology and morphometrics in the Garden Warbler *Sylvia borin* at the Ottenby Bird Observatory, Sweden

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Trapping and ringing near ecological barriers can provide useful information about the migration strategies of bird species. In this paper we analyzed ringing data of the Garden Warbler, collected within the period of 1950–2008 at the Ottenby Bird Observatory, south-eastern Sweden, and describe patterns in migration phenology, morphometrics and fuel load. A total of 4,351 individuals aged as either adults or juveniles were ringed during the period (yearly averages 7.3 adults and 83.1 juveniles) in addition to 1,514 birds of unknown age. Both age-specific and combined yearly totals did not significantly vary over the years. Median passage dates were 24 August, 30 August and 2 September for adults, juveniles and birds of unknown age, respectively. Median passage did not change significantly over the years. Among adults, larger individuals passed the observatory earlier than smaller individuals. The average fuel load was estimated at 24.3% of Lean Body Mass (LBM), and late-migrating individuals had higher fuel deposits than early migrants. Maximum fuel load was estimated at 82.5% of LBM; such an individual may be capable of a direct flight from Ottenby region to the Mediterranean area.

1. Introduction

The Garden Warbler *Sylvia borin* is a long-distance, trans-Saharan migrant that breeds in the Western Palaearctic region and winters over a wide range of areas in eastern, western and southern Africa (Cramp 1992). The migration of this species has been well documented in Europe (e.g., Fransson 1995, Totzke 1998, Grattarola 1999) and in sub-Saharan Africa (e.g., Ottosson *et al.* 2005, Smith 2007, Bayly & Rumsey 2010, Iwajomo *et al.* 2011). In Europe, ringing-recovery data indicate that the direction of migration is south to south-west in autumn, i.e., towards the Iberian

Peninsula, and from there individuals turn south to south-east towards the wintering grounds in sub-Saharan Africa (cf. Gwinner & Wiltschko 1978). The direction is reversed during spring migration (Cramp 1992). Thus, birds ringed in Sweden (and Finland) cross Europe via the Baltic region (Cramp 1992, Fransson & Hall-Karlsson 2008).

Most migratory bird species may land at favorable sites along their migratory flyway and fuel up before crossing inhospitable areas, such as seas and deserts. Many of these sites are located close to such ecological barriers. The Ottenby Bird Observatory (hereafter Ottenby) is one such stopover site for many bird species, particularly during autumn. The passage of songbirds through Ottenby provides an opportunity to study their migration. Consequently, the phenology of spring migration of Garden Warblers at Ottenby has been well documented (Fransson 1995, Stervander *et al.* 2005, Jonzén *et al.* 2006). However, information regarding the autumn migration of the species at Ottenby appears limited (Enquist & Pettersson 1986, Fransson 1995).

Trends in bird populations can be examined using data derived from ringing stations, especially where such data have been collected in a standardized manner over several decades. Several authors have used these sorts of data as complementary information regarding population changes (e.g., Helseth *et al.* 2005, Sanderson *et al.* 2006, Vorisek *et al.* 2008). Hence, the ringing data available at Ottenby presents an opportunity to contribute to current knowledge about the life history of the Garden Warbler.

The fuel used by migratory birds consists mostly of fat, which is primarily stored subcutaneously on the belly and in the tracheal pit (Alerstam & Lindström 1990) although protein is also oxidized during migration (e.g., Bauchinger & Biebach 1998, Jenni & Jenni-Eiermann 1998). From an optimization perspective, a migrating bird may either choose to migrate fast with large fuel deposits, or in short steps with just as much fuel as is necessary to reach the next stopover site (Alerstam & Lindström 1990). Birds that adopt the latter strategy may be faced with the challenge of when and where to refuel for the rest of the journey and how much fuel to deposit. These decisions become critical as the bird approaches ecological barriers, such as seas and deserts, as have been demonstrated in first-year Garden Warblers (Fransson *et al.* 2008).

For Garden Warblers crossing the Baltic Sea from Ottenby, there is ample opportunity to feed extensively before crossing the sea. Hence, the pattern in the fuel load of individuals at this site should give insights into the strategy they will adopt as they migrate. Autumn passage dates for this species at Ottenby have previously been published by Enquist and Pettersson (1986) and Fransson (1995) for the periods 1946–1984 and 1978–1990, respectively. However, in the present study we analyze a larger data set of autumn ringing at Ottenby; from 1950 to 2008. With these data we aim at describing the migration phenology and biometrics in the Garden Warbler during the autumn passage.

2. Material and methods

2.1. Trapping and ringing

The Ottenby Bird Observatory (56°12’N, 16°24’E) is situated on the southern point of Öland, an island in the Baltic ca. 10 km off the coast of south-eastern Sweden. Bergström and Svärdson (1938) made the first avian studies at this site in 1937–1938, and the observatory was founded ten years later, in 1946. Bird ringing was initially carried out during autumn seasons (1946–1948), and since 1949 also in the spring. From 1976 standardized trapping has been carried out yearly using a combination of the Heligoland traps and mist nets; 13 mist nets are used in autumn and 9 in spring. Since 1976, the standardized autumn-season trapping and ringing has taken place from 25 July to November 15 each year.

2.2. Morphometrics and phenology

A total of 6,045 individuals were available for analyses, of which 4,174 were juveniles (first year), 357 were adults (second year or older), and 1,514 birds were of unknown age. Since 1989 the body mass, measured to the nearest 0.1 g, has been recorded using either a Pesola spring balance or an electronic balance, while fat scores from 0 (no visible fat) to a maximum of 9 (a large amount of visi-

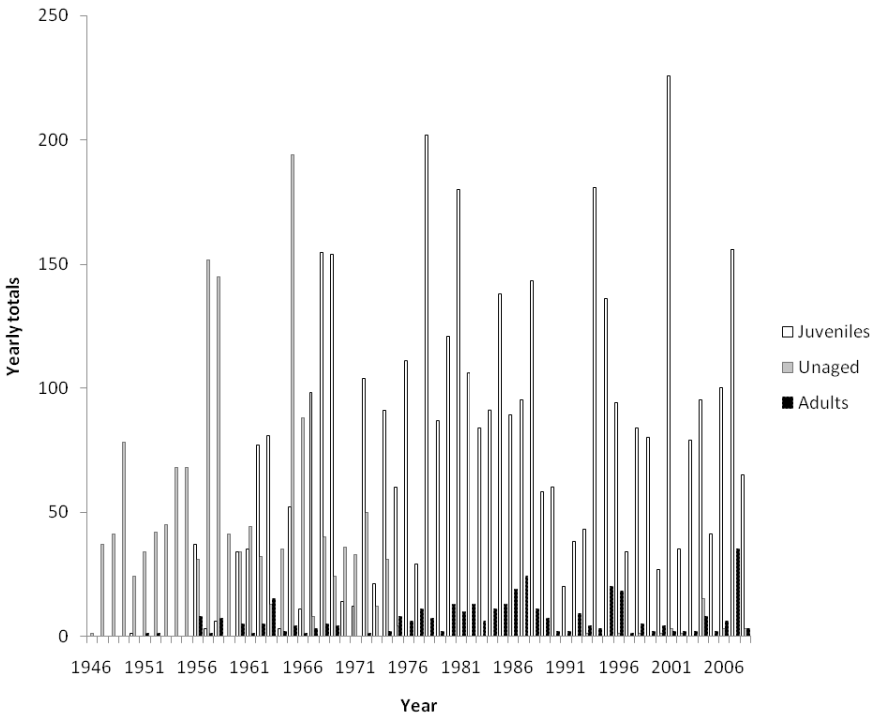

Fig. 1. Yearly total number of Garden Warblers ringed at the Ottenby Bird Observatory, Sweden, during the period 1956–2008. Data are based on years in which both adults and juveniles had been trapped. Black bars represent adults, gray bars represent unaged birds, and white bars represent juveniles.

ble fat) according to Pettersson and Hasselquist (1985) have been recorded. Wing lengths of trapped individuals have been measured to the nearest 1 mm using the maximum chord method (Svensson 1992, type 3).

Because not all the individuals in the present data had been trapped within the standardized autumn season, we confined the analyses to individuals trapped between 25 July and 15 November to allow for between-year comparisons. To analyze the trends in yearly total number of birds trapped, we included only those years in which both adult and juveniles were trapped, while for trends of median passage date, we included only years with at least five birds trapped in each age category.

Breast-muscle scores were not available for all individuals in the present data to allow the use of a recent method of estimating Lean Body Mass (LBM; Salewski 2009). Hence, we used the method described by Ellegren and Fransson (1992) to estimate size-specific LBM of captured birds. To achieve this, we classified the trapped birds based on wing length, into groups of at least 10 individuals of shared measure. For each group we related body mass to fat score by a linear regression and used relationship obtained to estimate an approximate value of the body mass corresponding to a fat score of zero for each wing-length class. These fat-free body masses were then related to their corresponding wing lengths by a second linear regression so as to obtain fat-free body-mass values for wing lengths outside the initial range. The size-specific LBM of each individual was derived from the residuals of the equation

$$\text{Size-specific LBM} = 0.19 \times \text{wing length} - 0.54 \quad (1)$$

Thereafter, we used the size-specific LBM to estimate the fuel load of each individual, expressed as percent of body mass measured.

Separate analyses were conducted for adults and juveniles (first-year birds) unless otherwise mentioned. Normality of data and homogeneity of variances were tested using Levene and Kolmogorov-Smirnov tests, respectively. Parametric correlation tests and GLM approaches (including classic ANOVA) were used if data did not violate the assumptions of normality, and when it did, non-parametric tests were used. Differences were considered significant at $P < 0.05$. All statistical analyses were conducted using SPSS Statistics 17.0 (SPSS Inc.).

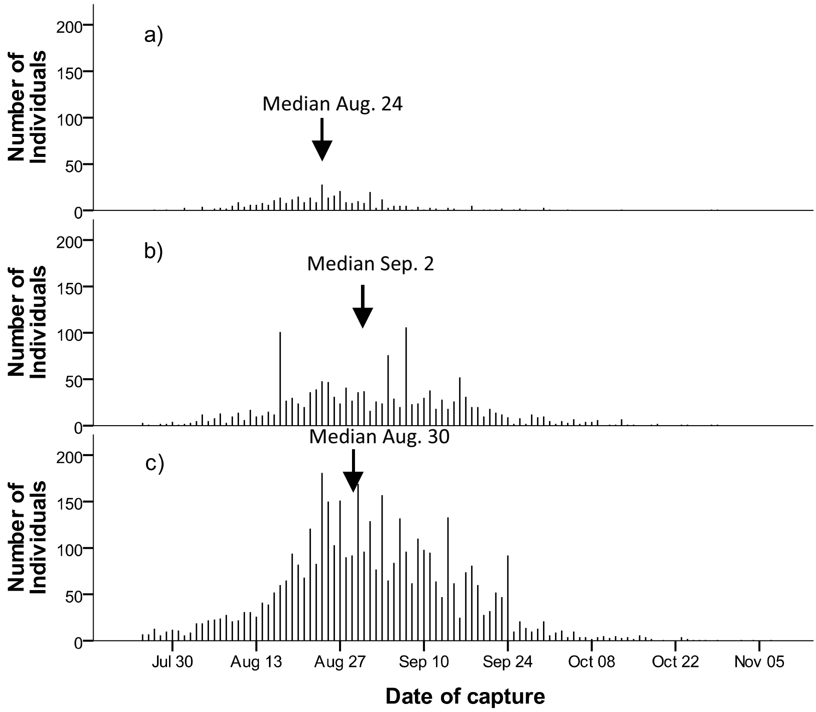

Fig. 2. Autumn migration phenology of (a) adult, (b) un-aged and (c) juvenile Garden Warblers trapped at the Ottenby Bird Observatory, Sweden.

3. Results

3.1. Annual ringing totals

There was a significant correlation between number of adults and juveniles trapped in each year (Spearman rank correlation; $r_s = 0.408$, $P = 0.004$, $n = 49$; Fig. 1). Based on our data, there was no significant trend in age-specific trapping numbers over the years (adults: $r_s = 0.60$, $P = 0.681$, $n = 49$; juveniles: $r_s = 0.220$, $P = 0.130$, $n = 49$). The total number of individuals ringed annually (age classes pooled) did not vary significantly over the years ($r_s = 0.212$, $P = 0.143$, $n = 49$). On average 83.1 ± 54.0 SD juveniles and 7.3 ± 6.9 SD adults were ringed each year.

3.2. Phenology of migration

The median passage dates were 24 August for adults, 30 August for juveniles and 2 September for birds of unknown age (Fig. 2). In combined data (age categories pooled), median date was 31 August. No significant trend was observed in the median passage date of adults and juveniles during 1950–2008 (adults: $r_s = -0.033$, $P = 0.869$, $n = 27$; juveniles: $r_s = -0.020$, $P = 0.893$, $n = 50$). The result was similar with age classes pooled ($r_s = 0.055$, $P = 0.702$, $n = 51$ trapping years).

3.3. Wing length, body mass and fuel load

Adults had longer wings than juveniles ($F_{1,1632} = 27.756$, $P<0.001$; adult mean 80.8 mm ± 2.1 SD, $n = 127$; juvenile mean 79.9 mm ± 2.0 SD, $n = 1{,}507$). The seasonal trend in wing length differed between the age classes ($F_{1,1630} = 4.059$, $P = 0.044$). Whereas the wing length of adults declined significantly as the season progressed ($F_{1,125} = 5.233$, $P = 0.024$, $B = -0.034$), that of juveniles did not change significantly ($F_{1,1505} = 1.577$, $P = 0.209$; Fig. 3). Body mass did not vary significantly between the two age classes ($F_{1,1644} = 0.278$, $P = 0.598$). Based on data with age classes pooled, the average body mass was 18.2 g ± 1.9 SD ($n = 1{,}688$). The structural size – measured as wing length – of adults differed from that of juveniles, body mass was significantly related to wing length ($F_{1,1644} = 32.61$, $P<0.001$, $B = 0.136$), and the slope of the relationship was not significantly different

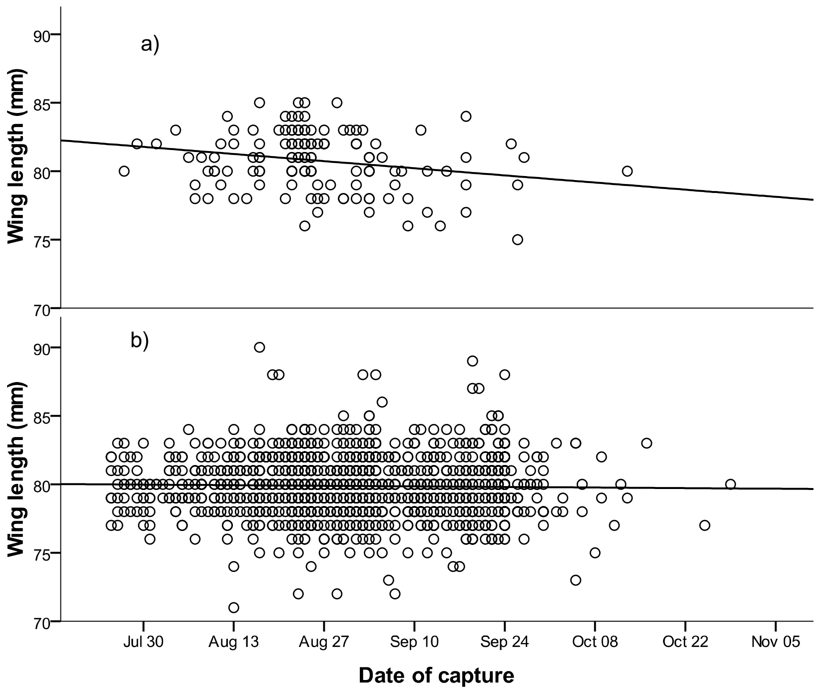

Fig. 3. Seasonal trend in wing length of (a) adult (n = 127) and (b) juvenile Garden warblers (n = 1,507) at the Ottenby Bird Observatory, Sweden.

between the two age classes, as indicated by the non-significant interaction term wing length × age ($F_{3,1642}$ = 11.16, P = 0.384). Hence, we derived the size-corrected estimate of the body mass for all birds, irrespective of age, from the residuals of a linear regression of body mass with wing length, described by the equation

Body mass = 7.0 + 0.136 × wing length (2)

The mean size-specific body mass of adults was higher than that of juveniles (adult mean = 18.0 g ± 0.29 SD, n = 134; juvenile mean = 17.9 g ± 0.27 SD, n = 1,512; $F_{1,1644}$ =24.537, P<0.001). The trend in size-specific body mass over the season differed between the two age classes ($F_{3,1642}$ = 11.42, P = 0.029). Over the season, size-specific body mass of adults declined ($F_{1,132}$ = 6.284, P = 0.013, B = –0.005), while that of juveniles showed no significant change ($F_{1,1510}$ = 2.016, P = 0.156).

The average fuel load was 24.3% of LBM. Of all the birds trapped, 1.4% had a negative fuel load. Fuel load increased significantly over the season (linear model, $F_{1,1644}$ = 14.94, P<0.001; Fig. 4). The maximum fuel load was estimated at 82.5% of LBM.

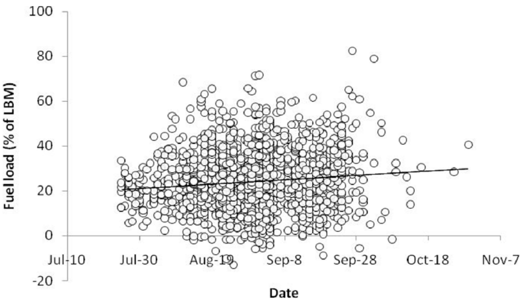

Fig. 4. Seasonal trend in fuel load (% of LBM) of autumn-migrating Garden Warblers (n = 1,646) at the Ottenby Bird Observatory, Sweden.

4. Discussion

4.1. Yearly totals and migration phenology

We found no significant trend in the number of trapped Garden Warbler individuals, either in the combined yearly or age-specific totals using only years in which both age classes were trapped. This was not an unexpected finding, considering that the Garden Warbler population has been relatively stable over much of Europe in the past four decades (e.g., Sanderson *et al.* 2006, Vorisek *et al.* 2008). It therefore seems that the species has maintained relatively stable breeding success on its Scandinavian or North European breeding grounds. It is worthy to note that on average more juveniles than adults were trapped each autumn, possibly reflecting the number of nestlings that successfully fledge each breeding season. A similar pattern has been reported for many autumn migrating species at Ottenby (Knape *et al.* 2009).

The phenology of autumn migration of songbirds is diverse: some species have shown advancement whereas others have delayed their median passage date. Tøttrup *et al.* (2006) reported no change in the median passage date of Garden Warblers, although there was an advanced departure amongst the last individuals. Also, Jenni and Keri (2003) showed that many long-distance migrants have advanced their peak autumn passage in recent years, although this depends on the species-specific number of, and variation in, broods raised per season. Kovács *et al.* (2011) have recently reported a 13-day advancement in the peak passage of Garden Warblers in Hungary. In the present study we found no change in autumn median passage date, a finding consistent with other reports (Nowalowski 2000, Tøttrup *et al.* 2006). The absence of a significant change in autumn phenology of birds at Ottenby may be due to their proximity to the Scandinavian or North European breeding grounds, whereas birds trapped in Hungary may be comprised of larger proportions of birds starting their migration from breeding grounds farther away.

The difference between adult and juvenile passage was 6 days. The median passage date estimated from pooled data of adults, juveniles and birds of unknown age (31 August) is 15 days earlier than the median date of recoveries of Garden Warblers in the Mediterranean area, about 3,000 km away (15 September; Fransson 1995). Considering that the median date for birds of unknown age (2 September) did not fall between that of adults and juveniles, many of the hitherto un-aged birds may be juveniles. Also, as about 25% of the total sample (1,514 birds) could not be aged as either adults or juveniles, the ageing criteria used for Garden Warblers at Ottenby should be revised.

4.2. Biometrics

In our study, the average body mass was lower than the uncorrected mass of first-year birds trapped in Greece (20 g; Fransson *et al.* 2008), supporting the fact that large fuel deposition occurs further south on the migratory route. Schaub and Jenni (2000) also reported a North-South and East-West gradient in the average body mass of Garden Warblers. Size-specific body mass of adult birds declined significantly towards the end of the season, but that of juveniles did not. This suggests that larger adults pass through our study site earlier than smaller ones. During autumn migration, in species which undergo a complete moult on their winter quarters, feathers are commonly old and worn in adults but new and fresh in juveniles. This pattern may result in the wing length of adults being shorter than that of juveniles. However, the current data showed that on average the wing length of adults was longer than that of juveniles, as has earlier been reported by Cramp (1992). This pattern suggests that the feathers of the majority of adults trapped at our study site were only slightly abraded and still longer than those of juveniles. We expect that by the time adult birds reach areas south from the Mediterranean Sea or Sahara desert, the level of wear in their feathers will be higher.

That the wing length of adults declined over the season while that of juveniles did not change significantly further reflects a size-dependent passage of adult birds. Larger individuals may have been able to establish territories and breed earlier and may then embark on their southward migration earlier than smaller individuals. Another possibility is that individuals with more worn-out feathers pass Ottenby later on in the season. It is unlikely that the early migration of larger individuals is sex-related, as both males and females incubate eggs (Cramp 1992). However, we do not have data on the sex of the individuals we studied.

4.3. Fuel load and migration strategy

The average fuel load of Garden Warblers migrating through our study site (24.3% of LBM) was similar to values estimated for many long-distance passerines wintering in the Tropics (e.g., Alerstam

& Lindström 1990, Fransson *et al.* 2008). This pattern of low fuel load has been suggested to be a response to factors such as flight costs associated with large fuel loads, as well as predation risks of foraging and maintenance (Alerstam & Lindstrom 1990, Klaasen & Lindstrom 1996, Kullberg *et al.* 1996). The maximum fuel load obtained in our study was higher than that reported for individuals at Gotland, south-eastern Sweden (43%; Ellegren & Fransson 1992). Although fuel load increased later on in the season, an expected response to a longer flight from Ottenby, it was still relatively low. For example, the average departure fuel load for first-year birds in Greece was nearly 100% of LBM (Fransson *et al.* 2008). These figures suggest that most Garden Warblers leaving Ottenby migrate in short steps, and that larger fuel reserves may only be built when they reach more demanding regions during the migration route (Fransson *et al.* 2001, Fransson *et al.* 2008). Also, individuals migrating late in the season may be constrained by time and so invest more on gaining fat, perhaps as an "insurance" against the uncertainty of conditions further south.

Assuming a wing span of 0.24 m, wing area of 0.011, aspect ratio of 5.24 and an altitude of 1,000 m in still air (Flight version 1.21; Pennycuick 1989), an individual with the maximum fuel load may be able to cover a distance of about 4,108 km, more than the distance to the Mediterranean area, which is about 3,000 km. Furthermore, the challenge posed by the Baltic Sea seems to be small, as the majority of Garden Warblers have low fuel loads, which probably is sufficient to reach the next stopover.

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Lehtokertun syksyinen fenologia ja mittavaihtelu Ottenbyssä, Ruotsissa

Lintujen pyydystäminen ja rengastus lähellä ekologisia esteitä kertovat paljon lintujen muuttostrategioista. Analysoimme lehtokertun (*Sylvia borin*) rengastusaineistoa, joka oli kerätty 1950–2008 Ottenbyn lintuasemalla Kaakkois-Ruotsissa, ja kuvailemme lajin muutonaikaista fenologiaa, mittatietoja ja energiavarantoja. Jakson aikana rengastettiin 4351 aikuista ja nuorta yksilöä (vuosittain keskimäärin 7,3 aikuista ja 83,1 nuorta), minkä lisäksi rengastettiin 1514 yksilöä ilman iänmääritystä. Ikäluokkien ja yhdistetyn aineiston määrät eivät vaihdelleet merkitsevästi vuosien välillä. Muuton mediaanipäivämäärät olivat 24.8. aikuisilla, 30.8. nuorilla ja 2.9. iälleen määrittämättömillä. Mediaanipäivä ei muuttunut tutkimusjakson aikana merkitsevästi. Isokokoisemmat aikuiset muuttivat pienikokoisempia aiemmin. Energiavaranto oli keskimäärin 24,3 % rasvattomasta massasta, ja myöhemmin muuttavilla arvot olivat korkeampia. Maksimienergiavaranto oli 82,5 % rasvattomasta massasta; tällainen yksilö saattaa suoriutua suorasta matkasta Välimeren alueelle.

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