Seasonal and diurnal increases in energy stores in migratory warblers at an autumn stopover site along the Asian–Australasian flyway

(Article begins on next page)

14 December 2021

Seasonal and diurnal increases in energy stores in migratory warblers at an autumn stopover site along the Asian-Australasian flyway

Martha Maria Sander[1], Wieland Heim[2], Heiko Schmaljohann[3,4]

E-mail: marthamaria.sander@unito.it

1 Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy

2 Institute of Landscape Ecology, University of Münster, Heisenbergstraße 2, 48149 Münster, Germany

3 Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, 26386 Wilhelmshaven, Germany

4 Institute for Biology und Environmental Sciences (IBU), Carl von Ossietzky University of Oldenburg, Carl-von-Ossietzky-Straße 9-11, 26129 Oldenburg, Germany

37

38   **Abstract:**

39   In contrast to the rapidly growing knowledge on migratory routes, wintering grounds, and timing of annual life

40   cycle events, the knowledge with respect to how songbirds refuel at stopover sites along the Asian-Australasian

41   flyway has increased only slowly, despite that migrant birds along this flyway show declining trends. We

42   analysed the amount and variation of energy stores between species, variation of energy stores within the day

43   and within the season, and estimated flight ranges of ten closely related warbler species (genera *Acrocephalus,*

44   *Arundinax*, *Locustella* and *Phylloscopus*), captured at a stopover site in the Russian Far East during autumn

45   migration. We found significant differences in species' energy stores, with Pallas's Leaf Warbler *Phylloscopus*

46   *proregulus* having by far the highest. All species increased their energy stores within the day, and eight species

47   increased their energy stores within the season. Individuals with the highest estimated flight ranges were able

48   to cover a distance of 470 km during one nocturnal flight bout, which would lead to a minimum of nine

49   stopovers before the birds reach their wintering grounds. We assume that a combination of multiple factors

50   shapes the variation in energy stores between the species. We discuss the potential of exploiting different

51   habitats, differences in refuelling strategy according to the distribution of species-specific refuelling habitats

52   along the migratory route, and the potential to exploit a variety of food resources. This study is the first to

53   provide information on energy stores, refuelling strategies and flight ranges for a set of closely related songbird

54   species migrating along the Asian-Australasian flyway.

55   **Deutsche Zusammenfassung**

56   Der Kenntnisstand zu den Zugwegen, den Winterquartieren und der zeitlichen Organisation des Jahreszyklus

57   ziehender Singvogelarten hat sich in den letzten Jahren stark verbessert. Weitaus weniger ist über die

58   Fettdeposition und die Rastökologie bekannt. Dies gilt insbesondere für Singvogelarten, welche entlang der

59   Ostasiatischen Route in ihre Winterquartiere ziehen. Hier vergleichen wir die Energiereserven von zehn

60   verschiedenen Arten aus den Gattungen *Acrocephalus, Arundinax*, *Locustella* und *Phylloscopus* an einem

61   Zwischenrastplatz im Fernen Osten Russlands während des Herbstzuges. Dabei analysieren wir Unterschiede

62 zwischen den Arten und im Verlauf des Tages und der Saison. Wir konnten signifikante zwischenartliche

63 Unterschiede in den Energiereserven finden, wobei Goldhähnchen-Laubsänger *Phylloscopus proregulus* die

64 höchsten Reserven aufwiesen. Alle Arten zeigten eine Zunahme im Tagesverlauf, und bei acht Arten konnten

65 wir eine signifikante Zunahme im Laufe der Herbstsaison feststellen. Basierend auf den beobachteten

66 Energiereserven konnten wir maximale Flugreichweiten berechnen, wobei die fettesten Individuen bis zu

67 470km in einer Nacht zurücklegen könnten. Damit müssten die Vögel mindestens neun Mal rasten, um ihre

68 Winterquartiere in Südostasien zu erreichen. Wahrscheinlich ist eine Vielzahl von Faktoren für die

69 zwischenartlichen Unterschiede in den Energiereserven relevant. Zum Einen sind die Habitate und die

70 verfügbare Nahrung in unserem Untersuchungsgebiet vermutlich von verschiedener Qualität für verschiedene

71 Arten. Zum anderen könnten die Arten unterschiedliche Zugstrategien aufweisen, je nach Verfügbarkeit des

72 bevorzugten Habitats entlang der Route. Diese Studie ist die erste, welche die Energiereserven und

73 Flugreichweiten einer Gruppe nah verwandter ziehender Singvogelarten im Asiatisch-Australasiatischen

74 Zugwegssystem untersucht.

75

76

77

78

79

80

81

82

83

84

85

Introduction

87 Bird migration is a fascinating phenomenon undertaken by billions of birds travelling up to tens of thousands of

88 kilometres between their breeding areas and wintering grounds twice a year (e.g., Hahn et al. 2009; Egevang et

89 al. 2010; Bairlein et al. 2012; Doren and Horton 2018). For landbirds, these global movements concentrate

90 along three major flyways: the Nearctic, the Palaearctic-African, and the Asian-Australasian flyway, respectively

91 (Newton et al. 2008). The miniaturisation of tracking devices, such as satellite transmitters and light-level

92 geolocators, has led to an explosion of tracking studies which has revolutionised our understanding of when

93 and along which routes birds migrate, and where they overwinter (for reviews see e.g. Newton et al. 2008;

94 Fiedler 2009; Bridge et al. 2011; 2013; Finch et al. 2017; McKinnon and Love 2018). Although there are many

95 studies that have investigated the movement ecology of migratory birds along the Asian-Australasian flyway,

96 including storks (Shimazaki et al. 2004; Higuchi 2012), raptors (Higuchi 2012), cranes (Higuchi et al. 2004),

97 waders (Takekawa et al. 2010; Reid et al. 2013; Bellio et al. 2017), gulls (Guo-Gang et al. 2014), and songbirds

98 (Koike et al. 2016; Yamaura et al. 2017; Heim et al. 2018a), the knowledge with respect to how songbirds

99 behave at stopover sites (locations where they rest and fuel between their migratory flight bouts) has

100 increased only slowly along this flyway. Although many field studies have significantly contributed to this

101 research area (e.g., Valchuk et al. 2005; Wang et al. 2006; Biserov and Medvedeva 2009; Fukai et al. 2010; Nam

102 et al. 2011; Leliukhina and Valchuk 2012; Yong et al. 2015, 1998; Sander et al. 2017; Senda et al. 2018; Bozó et

103 al. 2018a; Heim et al. 2018b), there is still a strong bias in terms of number of studies and therefore general

104 knowledge of songbirds' stopover ecology towards the Nearctic and the Palaearctic-African flyway. Since

105 songbird migrants spend far more time and energy during stopover than during migratory flights (Wikelski et al.

106 2003; Schmaljohann et al. 2012), we can learn from stopover ecology studies how songbirds organise their

107 migratory journey in terms of these two currencies, reviewed e.g. by Alerstam (2011), but little is known about

108 this for the Asian-Australasian flyway (Wang et al. 2006; Yong et al. 2015). To address this gap, we analysed

109 ringing data of ten closely related warbler species of the genus *Phylloscopus*, *Arundinax, Acrocephalus,* and

110 *Locustella* captured by mist-nets at a favourable stopover site at the southern border of their breeding range in

111 the Russian Far East during autumn migration.

112   The first objective of this study was to describe the amount and variation of energy stores between the

113   species. If biologically relevant differences were found this would potentially indicate differences in the general

114   movement ecology of the species (cf. Schaub and Jenni 2001; Stêpniewska et al. 2018). For the Palaearctic-

115   African flyway it has been shown, e.g. that three songbird migrants (Eurasian Reed Warbler *Acrocephalus*

116   *scirpaceus*, Sedge Warbler *A. schoenobaenus*, and Garden Warbler *Sylvia borin*) differed in their amount of

117   energy stores, rates of accumulating energy, and stopover durations in autumn (Schaub and Jenni 2001). It was

118   argued that Reed Warblers make use of low, but predictable, food resources which would yield low rates of

119   accumulating energy and thus explain the generally long stopover durations (Schaub and Jenni 2001). Stopover

120   durations were more variable in the closely related Sedge Warbler, probably because this species strongly

121   relies on its preferred diet (reed aphids) which is spatially and temporally unpredictable, but can be

122   superabundant (Bibby et al. 1976; Bibby and Green 1981, 1983; Schaub and Jenni 2001). The shortest stopover

123   durations and thus the highest rates of accumulating energy were found in Garden Warblers, which are both

124   probably related to the species' ability to switch between an arthropod and fruit diet (Schaub and Jenni 2001).

125   Thus, if we find differences in the energy stores between species, we can carefully relate these to potential

126   differences in their movement ecology.

127   The second objective was to assess whether the energy stores generally increase within the day and/or

128   within the season in a between-individual comparison. First, we predict that if birds experience favourable

129   feeding conditions at the stopover site, they will generally accumulate energy stores within the day (Delingat et

130   al. 2009). Second, we predict that birds arriving late in season will have higher energy stores than birds

131   captured early in the season probably to increase migration speed (Fransson 1998; Dänhardt and Lindström

132   2001).

133   The third objective was to estimate the potential flight range of the species based on the energy stores at

134   capture, the generally prevailing wind conditions, and the average night length (cf. Sander et al. 2017).

135   Potential flight ranges were restricted to the night, because all species are most likely nocturnal migrants

136   (Wang et al. 2019) and cf. Hansen (1954) and Dorka (1966) for closely related European species. With the third

137   objective, we intend to provide the first estimates of the average distance potentially covered per nocturnal

138   flight bout for the considered species along the flyway. The results on all three objectives will substantially

6

139 improve our understanding on the movement ecology of songbird migrants along the Asian-Australasian

140 flyway.

141

142 **Materials and Methods**

143 *Study site and capture protocols*

144 Birds were caught within the volunteer-based Amur Bird Project at Muraviovka Park in the Russian Far East

145 (49°55′08, 27′′N, 127°40′19,93′′E), cf. Heim and Smirenski (2013). This nature reserve includes wetlands,

146 meadows, and crop fields with small forest islands in the Amur River valley. Birds were trapped daily from local

147 sunrise to sunset during five autumn seasons (August–October 2011–2015). Up to 15 mist-nets (Ecotone,

148 Poland) with single lengths of six, twelve or 18 metres (mesh-size 16 or 30 mm), which added up to a total

149 length of maximal 148 metres, were placed in different habitats along a gradient from the low wetland to the

150 river terrace, including *Artemisia* thickets, willow-shrubs (e.g., *Salix miyabeana, S. pierotii*), forests of young oak

151 (*Quercus mongolica*) and poplar trees (e.g., *Populus tremula*) and a small pine plantation (*Pinus sylvestris*) (for

152 details see Heim et al. 2012, 2018a). We measured wing length (maximum chord) to the nearest 0.5 mm

153 (Svensson 1992) and body mass using an electronic balance to the nearest 0.1 g. We quantified the visible

154 subcutaneous fat on a nine-class scale (0–8, "fat score"; Kaiser 1993) and the size of the pectoralis muscle on a

155 four-class scale (0–3, "muscle score"; Bairlein 1995). After ringing, birds were released immediately.

156

157 *Energy stores*

158 We compared energy stores rather than body mass, because the ten warbler species differ substantially in their

159 size (range of wing lengths in this study 47–84.5 mm) and body mass increases allometrically with the size of

160 the bird, cf. Labocha and Hayes (2012). We estimated "lean" body mass from wing length using species-specific

161 linear regressions based on "lean" individuals with a fat score of 0 and a muscle score less than 3 of the

162 corresponding species. Birds were caught in the study area in the autumnal migratory seasons as mentioned

7

163   above and additionally during three spring seasons (April–June 2013, 2015, and 2016) to increase the

164   respective sample sizes:

165   "lean" body mass$_i$ [g] = a * wing length$_i$ [mm] + b   (1)

166   with a [in g/mm] as the slope and b [in g] as the intercept. In three species (Arctic Warbler *Phylloscopus*

167   *borealis*, Pale-legged Leaf Warbler *Phylloscopus tenellipes,* and Two-barred Warbler *Phylloscopus*

168   *plumbeitarsus*), the species-specific sample size of "lean" individuals was below ten. As "lean" body mass was

169   similarly related to wing length across these three species (see Electronic Supplementary Material 1a), we

170   pooled the data of "lean" individuals of these three species, to estimate how a change in wing length affects a

171   change in "lean" body mass. Results of all corresponding linear regressions are given in the Electronic

172   Supplementary Material 1b.

173   Energy stores were calculated for each individual by considering the species-specific regression

174   analysis to estimate the individual "lean" body mass as:

175   energy stores$_i$ = (body mass$_i$ [g] – "lean" body mass$_i$ [g])/"lean" body mass$_i$ [g]   (2)

176

177   *Flight range estimation*

178   Flight ranges (Y) were estimated following Delingat et al. (2009) according to the equation:

179   Y_i [km] = 100 * U [km/h] * ln (1+f_i)   (3)

180   with f_i as the individual energy stores$_i$ [from equation 2] and U as the generally assumed flight speed [in km/h].

181   Flight speed is the bird's speed in relation to the ground and is a function of the bird's air speed, i.e., its speed

182   relative to the air, and the influence of wind (Liechti 2006). To the best of our knowledge, there are no air

183   speed estimates available for the ten songbird species considered in this study. We therefore applied the

184   average air speed estimate of two congeneric species (Willow Warbler *Phylloscopus trochilus*: 9.5 m/s and

185   Marsh Warbler *Acrocephalus palustris*: 8.8 m/s, cf. Bruderer and Boldt (2001), which is 9.2 m/s (33 km/h), as an

186   approximate estimate for all species.

187   The influence of wind can be negative (head winds) or positive (tail winds) and is further influenced by

188   side wind (Kemp et al. 2012a). To account for the prevailing wind conditions and their effect on the flight range

189   estimates, we estimated the general wind conditions, i.e., flow assistance, at the study site towards the

190   wintering ground using the National Centres for Environmental Prediction Reanalysis II data from the National

191   Oceanic   and   Atmospheric   Administration   (NOAA,   Boulder,   CO,   USA;

192   http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.html (Kalnay et al. 1996). Wind data were obtained

193   via the R package "RNCEP" (Kemp et al. 2012b) and were shown to correlate well with real wind measurements

194   (Bromwich and Wang, 2005; Chelton and Freilich, 2005; Schmaljohann et al., 2009, 2011). The influence of

195   wind was quantified using equation[Airpseed] and following Kemp et al. (2012a):

196    $$flow\ assistance\ \left[\frac{m}{s}\right] = flow\ speed\ \left[\frac{m}{s}\right] * \cos(\theta) + \sqrt{z^2 - (y * \sin(\theta))^2} - z \qquad (4)$$

197   with θ is the angular difference between the direction into which the wind is blowing and the bird's migratory

198   direction towards its general wintering ground. The latter was estimated by calculating the average centres of

199   the wintering ranges for each species; data were derived from the IUCN range maps (BirdLife International

200   2017). Species' average centre of the wintering range was simplified as the mean of the northernmost and

201   southernmost latitude and the eastern- and westernmost longitude. Since the wintering ranges of the ten

202   species coincide to a large extent (varying only from 25°–5° N and 113°–91° E; BirdLife International 2017, the

203   preferred migratory direction of all study species was set to the overall corresponding mean value, i.e. 14° N

204   and 104° E. z is bird's speed [in m/s] relative to the wind. Y is wind speed [in m/s]. We applied the "NCEP.flight"

205   function of the R package "RNCEP" (Kemp et al. 2012a) with "flow.assist" set to "NCEP.Airspeed", "air speed"

206   set to 9.2 m/s (see above) and "path" to "great circle". As all ten warbler species probably migrate exclusively

207   during the night (Wang et al. 2019), flow assistance was estimated for the average night length the birds

208   experienced during the field study, which was eleven hours. The assumption that the warblers migrated only

209   during the night seems reasonable, because most songbirds setting off with high energy stores and towards the

210   seasonally appropriate migratory direction start their migratory flight bout shortly after sunset (Müller et al.

211   2016, 2018) and terminate it shortly before sunrise (Liechti et al. 2018). Thus, "hours" was set to 11 and

212   "evaluation.interval" to 220 min (3 downloads per night).

213   For further analyses, we obtained the best flow assistance of four different pressure levels (1000, 925,

214   850, and 700 mbar) (cf. Liechti 2006; Schmaljohann et al. 2009; Mateos-Rodríguez and Liechti 2012), a bird

215   could have potentially experienced towards the assumed centre of the wintering range during each evaluation

216   interval, since many songbird species depart from stopover when wind conditions, i.e. flow assistance, are

217   favourable (reviewed in Liechti 2006; Shamoun-Baranes et al. 2017). We calculated the mean of these three

218   flow assistance estimates per night, so that we obtained one average value per night. Visual inspection of these

219   values did not show any trend of flow assistance with day of year (see Electronic Supplementary Material 2).

220   Therefore, we considered the 75%-quartile, i.e. the best 25 % of these values, of flow assistance to capture the

221   probable wind conditions the ten warbler species experienced during their potential nocturnal migratory flight

222   when "departing" from the study site. Although this is of course a simplification, this approach seems feasible,

223   because songbirds are known to generally time their departure from stopover to coincide with favourable wind

224   conditions (Dierschke and Delingat 2001; Erni et al. 2002; Schmaljohann et al. 2017) and also adjust their flight

225   altitude to these (Schmaljohann et al. 2009; Shamoun-Baranes et al. 2017). Most of the studied warbler species

226   were found to migrate mostly with favourable winds at our study site (Bozó et al. 2018a). Negative flight range

227   estimates were set to zero.

228   Migration distance was defined as the great circle distance between the location of the study site and

229   the centre of the wintering range (based on BirdLife International 2017 range maps, see Electronic

230   Supplementary Material 3). To estimate the potential number of stopovers required to reach the latter, we

231   neglected the geographical differences of the species' winter distribution and assumed furthermore that the

232   birds would always resume migration with the same energy stores and would not continue their flight into the

233   day time. This assumption, i.e., the level of refuelling is similar at each stop over site, seems reasonable

234   because birds do not have to cross major ecological barriers, such as mountains, deserts, and/or the sea, but

235   migrate across benign habitats towards their migratory destination. It, thus, seems rational that the common

236   migration strategy of these migrant birds can be described as performing alternating cycles of accumulating

237   relatively low energy stores during stopover and flying for a single night.

238

Statistical analyses

240   Statistical analyses were performed using the R 3.4.2 statistical software package (R Core Team). Day of capture

241   was transformed to day of year (1 = 1 January).

242   Variation in energy stores between species was modelled using a linear mixed effect model (LMM)

243   assuming normally distributed errors. "Species" was included as the explanatory variable. "Year" was included

244   as a random factor (intercept) to account for potential differences between the years.

245   Variation in energy stores within the day was modelled separately for each species using a LMM

246   assuming normally distributed errors. Each model included "hours after sunrise" as the explanatory variable.

247   "Year" was included as a random factor (intercept), see above.

248   Variation in energy stores within the season was modelled separately for each species using a LMM

249   assuming normally distributed errors. Each model included "day of year" as the explanatory variable. "Year"

250   was included as a random factor (intercept), see above.

251   Residual analyses of all models did not show any violation of model assumptions. To assess

252   uncertainty of the model estimates and model predictions, we used Bayesian methods to obtain uncertainty

253   estimates of the model parameters (Korner-Nievergelt et al. 2015). We used improper prior distributions,

254   namely $p(\beta)\sim 1$ for the coefficients and $p(\sigma)\sim 1/\sigma$ for the variance parameters in all models, following Korner-

255   Nievergelt et al. (2015). To obtain posterior distributions of the respective models, we directly simulated 5000

256   values from the joint posterior distributions of each model's parameters applying the function "sim()" of the R-

257   package "arm" (Gelman and Hill 2007). We used the means of the simulated values from the joint posterior

258   distributions of each model's parameters as the respective model estimates, and the 2.5% and 97.5% quantiles

259   as limits for the 95% credible intervals (CrI), following Korner-Nievergelt et al. (2015). We declare an effect to

260   be significant if the corresponding 95% CrI does not include zero or if the 95% CrIs of the comparing groups do

261   not overlap.

262

263   **Results**

264   In total, 5,948 individuals were included in this study. Each species was caught in each year during the study

265   period. With 120 individuals the Pale-legged Leaf Warbler was the rarest and with 2,125 individuals the Yellow-

266   browed Warbler *Phylloscopus inornatus* was the most abundant species during the autumn seasons in 2011–

267   2015 (for sample sizes for all species see Fig. 1).

268

269   *Variation in energy stores between species*

270   Energy stores were found to differ significantly between the ten study species (Figs. 1). The energy stores were

271   highest in the Pallas's Leaf Warbler *Phylloscopus proregulus*, with a mean of 0.097 (95% CrI: 0.086, 0.108) and

272   lowest in the Two-barred Warbler, with a mean of -0.003 (95% CrI: -0.018, 0.11). According to the distribution

273   of the 95% CrIs of the species' energy stores (Fig. 1), the Two-barred Warbler did not have significantly

274   different energy stores than the Black-browed Reed Warbler *Acrocephalus bistrigiceps* and the Thick-billed

275   Warbler *Arundinax aedon*, while the energy stores of the remaining species were all significantly higher than in

276   the Two-barred Warbler. In addition, the Arctic Warbler had significantly higher energy stores than the Black-

277   browed Reed Warbler, the Thick-billed Warbler, the Yellow-browed Warbler, and the Radde's Warbler

278   *Phylloscopus schwarzi*, but significantly lower energy stores than the Pallas's Leaf Warbler (Fig. 1).

279

280   *Variation in energy stores within the day*

281   At sunrise, birds were generally in lean body condition, cf. Tab. 1, Fig. 2. Energy stores significantly increased

282   within the day in all species (Tab. 1, Fig. 2). The strongest increase was found in Pallas's Leaf Warblers, which

283   increased their energy stores from 0.8 % to 4.4 % of the bird's "lean" body mass (0.011 h^{-1}, 95% CrI: 0.010 h^{-1},

284   0.013 h^{-1}) within the day, and in Pale-legged Leaf Warblers (0.011 h^{-1}, 95% CrI: 0.007 h^{-1}, 0.014 h^{-1}). The lowest

285   increase was found in Pallas's Grasshopper Warbler *Locustella certhiola* (0.005 h^{-1}, 95% CrI: 0.003 h^{-1}, 0.007 h^{-1}),

286   Black-browed Reed Warbler (0.006 h^{-1}, 95% CrI: 0.004 h^{-1}, 0.008 h^{-1}), and Radde's Warbler (0.005 h^{-1}, 95% CrI:

287   0.002 h^{-1}, 0.008 h^{-1}) (Tab. 1, Fig. 2).

288

289 *Variation in energy stores within the season*

290 At the beginning of the autumnal migration season, birds were in rather lean condition, as expressed by the

291 low energy stores (Tab. 2, Fig. 3). For all but two, the Arctic Warbler and Two-barred Warbler, energy stores at

292 capture significantly increased between individuals within the season and varied from 0.0006 to 0.0024 per day

293 (Tab. 2, Fig. 3). The strongest increase was found in the Radde's Warbler (0.0024 day^{-1}, 95% CrI: 0.0013 day^{-1},

294 0.0034 day^{-1}), which showed an increase of 1.1 % of bird's "lean" body mass within 54 days (difference of day

295 of first capture and day of last capture considering all years), and the Pale-legged Leaf Warbler (0.0023 day^{-1},

296 95% CrI: 0.0006 day^{-1}, 0.0038 day^{-1}), which showed an increase of 0.9 % of bird's "lean" body mass within 34

297 days. The lowest increase was found in the Dusky Warbler *Phylloscopus fuscatus* (0.0006 day^{-1}, 95% CrI: 0.0003

298 day^{-1}, 0.0008 day^{-1}) with an increase of 0.5 % of bird's "lean" body mass within 71 days (Tab. 2, Fig. 3).

299

300 *Potential flight range*

301 Potential flight range of all individuals of all species captured at the study site varied from 0 to 1,300 km (Fig.

302 4). The median potential flight ranges per species varied from 0 to 360 km. The former belongs to the Two-

303 barred Warbler (25% and 75%-quantile: 0 and 120 km), while the latter belongs to the Pallas's Leaf Warbler

304 (25% and 75%-quantile: 205 and 530 km). A certain proportion of each species (highest in Pallas's Leaf Warbler

305 with 32 % of captured individuals) would have been able to fly for the entire night (10 hours) and to cover a

306 distance of more than 470 km in one flight bout (Fig. 4). These birds would have to stop approximately nine

307 times (considering a migration distance of ~ 4,000 km, BirdLife International 2017) during autumn migration to

308 reach their assumed centre of the wintering range.

309

310 **Discussion**

311 Our study clearly demonstrates that the ten warbler species significantly differed in their energy stores at

312 capture at our stopover site in the Russian Far East (Fig. 1). Assuming that the between-individual effects

313 quantified in our approach (Figs. 2, 3) agree with the effects acting at the individual level, we further found that

13

314 the species varied significantly in their degree of change in energy stores over time, i.e., within the day and

315 within the season (Figs. 2, 3). The Pallas's Leaf Warblers carried the highest energy stores and had the strongest

316 increase in energy stores within the day and within the season (Figs. 1 – 3). The Two-barred Warbler, in

317 contrast, had low energy stores and these were hardly affected by time of the day and day of the year (Figs. 1 –

318 3). This strongly suggests that there are probably significant differences in the stopover ecology between the

319 species, with Pallas's Leaf Warbler being probably able to switch to more commonly food sources, while the

320 Two-barred Warbler and Pallas's Grasshopper Warbler are probably more stenoecious species (cf. Schaub and

321 Jenni 2001; Stêpniewska et al. 2018).

322

323 *Variation in energy stores between species*

324 The significant species-specific differences in the energy stores are probably related to specific habitat

325 requirements and/or migration strategies. Although all considered species are mainly insectivorous, the study

326 site may offer species-specific refuelling conditions, because some species may have a broad or narrow niche

327 concerning the habitats in which they forage during stopover. Previous work found supportive evidence for this

328 assumption and detailed that some warblers occur in many different habitats at our study site, while others

329 seem to be more specialised (Bozó et al. 2018b). The majority of Pallas's Leaf Warblers was captured in

330 deciduous forest, pine forest, and shrubs. As this species showed the highest energy stores of all warbler

331 species, we carefully argue that the potential of exploiting different habitats may be one reason why the

332 species showed high energy stores (Tab. 1, Figs. 1) and increased these within the day and within the season so

333 strongly (Tabs. 1, 2, Figs. 2, 3). The Thick-billed Warbler is known to forage in reeds and willow shrubs close to

334 water (del Hoyo and Christie 2006). However, its abundance was not related to a certain habitat type at our

335 study site (Bozó et al. 2018b), which may indicate that the species feeds in a high variety of different habitats

336 during migration. Despite this, energy stores and their changes within the day and within the season were not

337 especially pronounced (Tabs. 1, 2, Figs. 1 - 3). The Pallas's Grasshopper Warbler and the Black-browed Reed

338 Warbler, in contrast, were only abundant in the reeds (Bozó et al. 2018b) and had relatively low energy stores

339 (Tab. 1, Fig. 1). Although the range and types of habitats used during stopover may be indicative for the more

340 general pattern in energy store change over time, i.e. day and season, there are other factors, e.g., the

14

341 potential of exploiting a variety of food resources, explaining the variation in energy stores between the

342 species and over time which we did not cover in this study. In summary, we assume a combination of multiple

343 factors (the potential of exploiting different habitats, differences in the refuelling strategy according to the

344 distribution of species-specific refuelling habitats along the migratory route, the potential of exploiting a

345 variety of food resources) jointly shape variation in energy stores between the species.

346   We therefore assume that the between-species differences in energy stores and change over time

347 may also result from species-specific refuelling strategies. The variety of habitats which could be potentially

348 exploited for refuelling and their distribution along the migratory route may determine to which extent the

349 species refuel at a given stopover site (Schaub and Jenni 2001). Species refuelling to a larger extent (i.e. Pallas's

350 Leaf Warbler; Tabs. 1, 2, Figs. 1 - 3) may increase the distance covered by the next flight bout because they

351 might be more restricted to certain habitat types (e.g., Pallas's Leaf Warbler, forest and shrubs) than others

352 (e.g. Thick-billed Warbler, Radde's Warbler) (Bozó et al. 2018b).

353   The degree of food-specialisation, and thus if they are more opportunistic than others, may also

354 determine species' migration strategy. The variety of food resources the species can use (insects only or insects

355 and fruits) and the ability to switch between these related to their abundance may influence refuelling patterns

356 (Schaub and Jenni 2001). In contrast to the Leaf Warblers, Grasshopper and Reed Warblers are both able to

357 include vegetable material into their diet (del Hoyo and Christie 2006), which means, they are more variable in

358 their foraging habits and may have more predictable resources. Pallas's Leaf Warblers and Arctic Warblers prey

359 on insects (high energy stores, Fig. 1) whereas Black-browed Reed Warblers, Pallas's and Grasshopper Warblers

360 (and possibly Black-browed Reed Warblers as well) include vegetable material into their diet during migration

361 (Dement'ev and Gladkov 1954) (low energy stores, Fig. 1). Since very little information is available on food

362 requirements of the studied taxa during stopover, it is difficult to assess how variation in food requirements

363 may affect their migration strategy along the Asian-Australasian flyway.

364   Relating these findings to the refuelling patterns of different warblers discussed in Schaub and Jenni

365 (2001), we conclude that Pallas's Leaf Warblers might depend more strongly on the presence of specific

366 habitats, which they find and further exploit at a higher rate at our study site (Fig. 2). Other species, such as the

367   Thick-billed Warbler and the Radde's Warbler, may find suitable stopover sites more regularly along the route,

368   as they are found to be more generalistic.

369   The estimates of energy stores differ from the true values because the individual lean body mass was

370   approximated by the bird's wing length only but not individually measured for each bird, cf. Guglielmo et al.

371   (2011). Furthermore, migratory birds may reversible fasten below their lean body mass (Salewski et al. 2010),

372   so that the measured/estimated lean body mass differs from the true value. Both issues may over- and

373   underestimate the energy stores. In addition, mist-netting data is probably biased towards lean birds because

374   foraging activity is condition-related resulting in a higher probability of catching the more mobile individuals.

375   The generally low energy stores (Fig. 1) maybe a specific phenomenon of our study site where birds do not

376   encounter any major ecological barrier before and after stopping there and thus do not have the urge to

377   accumulate high amounts of energy.

378

379   *Variation in energy stores within the day*

380   Many migratory songbirds perform a stop-and-go strategy (Åkesson and Hedenström 2007) and build up

381   energy stores during the day (Delingat et al. 2009), while migrating in the night (Dorka 1966; Müller et al.

382   2016). With the between-individual approach in our study we intended to approximate the within-individual

383   effects of time of day on the energy stores. (Delingat et al. 2009) have shown that the first-traps-by-time-of-

384   day-method (linear relationship between body mass and time of day) may not always be applicable to describe

385   the individual increase in energy stores in migrating birds during stopover. They have also shown that,

386   especially in low-sized samples, an increase in body mass within the day is rarely found in a between-individual

387   approach. Despite this, we found such an effect in all species (Tab. 1, Fig. 2). If our between-individual

388   approach correctly reflects the individual increase in energy stores within the day, birds build up more energy

389   stores than they lose during the night. This indicates that the study site is an important refuelling area

390   highlighting its significant status for conservation. Differences in the degree of refuelling (increase in energy

391   stores, Tabs. 1, 2, Figs. 2, 3) may be related to the species-specific foraging habitat (see above), but species of

392   the same foraging habitat (del Hoyo and Christie 2006; Glutz von Blotzheim and Bauer 1991) did not always

393   have a similar increase of energy stores within the day (Fig. 3). The Pallas's Leaf Warbler forages in the canopy

394   and was found to have the strongest increase, while the Pale-legged Leaf Warbler, which was also found to

395   have a strong increase, forages closer to the ground, similar to the Radde's Warbler, which had the lowest

396   increase of energy stores within the day. The mechanisms of refuelling in these small migratory passerines, and

397   whether they are able to switch the preferred diet in relation to abundance of food, remain unknown. With our

398   study, we have provided the first descriptive results which can be compared with patterns found in prospective

399   studies on these species and in this region.

400

401   *Variation in energy stores within the season*

402   The variation in energy stores within the day was stronger than the seasonal and the variation explained by

403   hours after sunrise was greater than that explained by day of the year (Tab. 1, 2, Fig. 2, 3). Nevertheless, we

404   found an increase in energy stores and thus increasing flight ranges within the season in eight species (Tab. 2,

405   Fig. 3). Similar patterns were found in e.g. Garden Warblers *Sylvia borin* and Northern Wheatears *Oenanthe*

406   *oenanthe* (Bairlein 1998; Corman et al. 2014), and other songbird species migrating along the Asian-

407   Australasian flyway, such as the Red-flanked Bluetail *Tarsiger cyanurus* (Wang et al. 2006) and *Luscinia* thrushes

408   (Biserov and Medvedeva 2009). The between-individual increase in energy stores within the season agrees with

409   the idea that birds tend to maximise migration speed when being late in season (Fransson 1998). Birds are

410   thought to exploit favourable refuelling sites more intensively, leading to high rates of energy accumulation

411   and thus high migration speeds (cf. Alerstam and Lindström 1990; Lindstrom and Alerstam 1992). Speeding up

412   migration may allow birds to counterbalance the upcoming seasonal temperature decrease and hence

413   diminishing insectivorous food sources within the season, and the increasing competition for habitats at the

414   wintering grounds, at least for species that defend territories there.

415

416   *Potential flight range*

417   In eight of our studied species, birds with the highest energy stores would have been able to fly throughout the

418   whole night (Fig. 4). Such high energy stores could indicate that they cover relatively long distances during the

17

419 nocturnal migratory flight bout, and thus minimise the number of stopovers required to reach the wintering

420 range. In the Pallas's Leaf Warbler, birds with high energy stores (75%-quantile, Fig. 4) could cover a distance of

421 over 500 km in one flight bout and thus might have energy stores left after the nocturnal flight. This could be

422 interpreted as a margin of safety in case of unfavourable weather and/or feeding conditions at the next

423 stopover site (Moore and Aborn 1996). Birds having lower energy stores than required for a whole night-time

424 flight (Two-barred Warbler, Black-browed Reed Warbler, Fig. 4) either will depart with lower energy stores

425 from the current stopover site to search for better refuelling opportunities in the surroundings, so called

426 "landscape movements", or are not in the condition for departure and thus stay and prolong their stopover

427 duration until sufficient energy is stored, reviewed in Schmaljohann and Eikenaar (2017).

428

429 **Conclusion**

430 This explorative investigation on ten conspecific small long-distance migrants fills an imminent knowledge gap

431 concerning the refuelling patterns at a stopover site along the Asian-Australasian flyway. Even though the

432 underlying mechanisms of the movement ecology of the species found at the study site are still unknown, we

433 found significant differences in their energy stores suggesting that they differ in their ability to exploit the

434 stopover site, or that they perform different refuelling strategies. Studying how birds organise their migration

435 along the Asian-Australasian flyway is important, as migrant birds along this flyway are showing declining

436 trends (Yong et al. 2015), and the conditions are deteriorating due to urbanisation and industrialisation

437 (Alauddin and Quiggin 2008), increasing agriculture intensification, climate change and unsustainable harvest

438 (Edenius et al. 2017; Kamp et al. 2015). Research on migration routes and stopover sites is of imminent

439 conservation concern, as suitable stopover habitats to rest and forage are crucial for the successful connection

440 between wintering and breeding ranges and furthermore for the protection of migratory species (Kirby et al.

441 2008).

442

443

444   References

445   Åkesson, S, Hedenström, A (2007) How Migrants Get There: Migratory Performance and Orientation.
446   BioScience 57:123–133

447   Alauddin, M, Quiggin, J (2008) Agricultural intensification, irrigation and the environment in South Asia: Issues
448   and policy options. Ecol. Econ. 65:111–124

449   Alerstam, T (2011) Optimal bird migration revisited. J. Ornithol. 152:5–23

450   Alerstam, T, Lindström, A (1990) Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety.
451   In Bird Migration, E. Gwinner, ed. (Berlin, Heidelberg: Springer)

452   Bairlein, F (1998) The Effect of Diet Composition on Migratory Fuelling in Garden Warblers *Sylvia borin*. J. Avian
453   Biol. 29:546

454   Bairlein, F, Norris, DR, Nagel, R, Bulte, M, Voigt, CC, Fox, JW, Hussell, DJT, Schmaljohann, H (2012) Cross-
455   hemisphere migration of a 25 g songbird. Biol. Lett. 8:505–507

456   Bairlein, F (1995) Manual of field methods. Revised edition. (Wilhelmshaven, Germany)

457   Bellio, M, Minton, C, Veltheim, I (2017) Challenges faced by shorebird species using the inland wetlands of the
458   East Asian-Australasian Flyway: the little curlew example. Mar. Freshw. Res. 68:999–1009

459   Bibby, CJ, Green, RE (1981) Autumn Migration Strategies of Reed and Sedge Warblers. Ornis Scandinavica 12:1–
460   12. https://doi.org/10.2307/3675898.

461   Bibby, CJ, Green, RE (1983) Food and Fattening of Migrating Warblers in Some French Marshlands. Ringing &
462   Migration 4 (3):175–84. https://doi.org/10.1080/03078698.1983.9673803.

463   Bibby, CJ, Green, RE, Pepler, GRM, Pepler, PA (1976) Sedge Warbler Migration and Reed Aphids. British Birds
464   69:384–99

465   BirdLife International (2017). IUCN Red List for birds

466   Biserov, M, Medvedeva, E (2009) The autumn migration of birds of genus *Luscinia* on Hingano-Bureya higland.
467   In Proceedings of the IV. Conference on current problems of Ornithology in Siberia and Central Asia, (Ulan-
468   Ude), 131–136

469   Bozó, L, Csörgő, T, Heim, W (2018a) Weather conditions affect spring and autumn migration of Siberian leaf
470   warblers. Avian Res. 9 (33):1–8

471   Bozó, L, Heim, W, Csörgő, T (2018b) Habitat use by Siberian warbler species at a stopover site in Far Eastern
472   Russia. Ringing Migr. 33:31–35

473   Bridge, ES, Thorup, K, Bowlin, MS, Chilson, PB, Diehl, RH, Fléron, RW, Hartl, P, Kays, R, Kelly, JF, Robinson, WD,
474   et al. (2011) Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds.
475   BioScience 61:689–698

476   Bridge, ES, Kelly, JF, Contina, A, Gabrielson, RM, MacCurdy, RB, Winkler, DW (2013) Advances in tracking small
477   migratory birds: a technical review of light-level geolocation: Light-Level Geolocation Dataloggers. J. Field
478   Ornithol. 84:121–137

479   Bromwich, DH, Wang, S-H (2005) Evaluation of the NCEP–NCAR and ECMWF 15- and 40-Yr Reanalyses Using
480   Rawinsonde Data from Two Independent Arctic Field Experiments*. Mon. Weather Rev. 133:3562–3578

481   Bruderer, B, Boldt, A (2001) Flight characteristics of birds: I. radar measurements of speeds. Ibis 143:178–204

482   Chelton, DB, Freilich, MH (2005) Scatterometer-Based Assessment of 10-m Wind Analyses from the Operational
483   ECMWF and NCEP Numerical Weather Prediction Models. Mon. Weather Rev. 133:409–429

484   Corman, A-M, Bairlein, F, Schmaljohann, H (2014) The nature of the migration route shapes physiological traits
485   and aerodynamic properties in a migratory songbird. Behav. Ecol. Sociobiol. 68:391–402

486   Dänhardt, J, Lindström, Å (2001) Optimal departure decisions of songbirds from an experimental stopover site
487   and the significance of weather. Anim. Behav. 62:235–243

488   del Hoyo, JE, and Christie, DA (2006) Old World Flycatchers to Old World Warblers. In: Handbook of the Birds of
489   the World. Barcelona, (Barcelona: Lynx Edicions)

490   Delingat, J, Dierschke, V, Schmaljohann, H, Bairlein, F (2009) Diurnal patterns of body mass change during
491   stopover in a migrating songbird, the northern wheatear *Oenanthe oenanthe*. J. Avian Biol. 40:625–634

492   Dement'ev, GP, Gladkov, NA (1954) Birds of the Soviet Union. (Moscow: Sovetskaya Nauka), p. 303

493   Dierschke, V, and Delingat, J (2001) Stopover behaviour and departure decision of northern wheatears,
494   *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behav. Ecol. Sociobiol. 50:535–545

495   Van Doren, BM, Horton, KG (2018) A continental system for forecasting bird migration. Science 361
496   (6407):1115–1118

497   Dorka, V (1966) Das jahres-und tageszeitliche Zugmuster von Kurz-und Langstreckenziehern nach
498   Beobachtungen auf den Alpenpässen Cou/Bretolet (Wallis) Ornithol. Beob. 63: 165–223.Edenius, L, Choi, C-Y,
499   Heim, W, Jaakkonen, T, De Jong, A, Ozaki, K, Roberge, J-M (2017) The next common and widespread bunting to
500   go? Global population decline in the Rustic Bunting *Emberiza rustica*. Bird Conserv. Int. 27:35–44

501   Egevang, C, Stenhouse, IJ, Phillips, RA, Petersen, A, Fox, JW, Silk, JRD (2010) Tracking of Arctic terns Sterna
502   paradisaea reveals longest animal migration. Proc. Natl. Acad. Sci. 107:2078–2081

503   Erni, B, Liechti, F, Underhill, LG, Bruderer, B (2002) Wind and rain govern the intensity of nocturnal bird
504   migration in central Europe - a log-linear regression analysis. Ardea 90 (1):155–166

505   Fiedler, W (2009) New technologies for monitoring bird migration and behaviour. Ringing Migr. 24:175–179

506   Finch, T, Butler, SJ, Franco, AMA, Cresswell, W (2017) Low migratory connectivity is common in long-distance
507   migrant birds. J. Anim. Ecol. 86:662–673

508   Fransson, T (1998) A feeding experiment on migratory fuelling in whitethroats, *Sylvia communis*. Anim. Behav.
509   153–162

510   Fukai, N, Sugawa, H, Chiba, K, and Ozaki, K (2010) Report on Japan-Russia Bird Banding Expedition on
511   Kamchatka Peninsula. Bull Jpn Bird Banding Assoc 8–36

512   Gelman, A, and Hill, J (2007) Data analysis using regression and hierarchical/multilevel models. N. Y. NY Camb

513   Guglielmo, CG, McGuire, LP, Gerson, AR, and Seewagen, CL (2011). Simple, rapid, and non-invasive
514   measurement of fat, lean, and total water masses of live birds using quantitative magnetic resonance. J
515   Ornithol 152, 75.

516   Glutz von Blotzheim, UN, Bauer, KM (1991) Handbuch der Vögel Mitteleuropas. (Wiesbaden: AULA-Verlag)

517 Guo-Gang, Z, Dong-Ping, L, Yun-Qiu, H, Hong-Xing, J, Ming, D, Fa-Wen, Q, Jun, L, Tian, M, Li-Xia, C, Zhi, X, et al.
518 (2014) Migration routes and stopover sites of Pallas's Gulls *Larus ichthyaetus* breeding at Qinghai Lake, China,
519 determined by satellite tracking. Forktail 30:104–108

520 Hahn, S., Bauer, S., Liechti, F. (2009). The natural link between Europe and Africa - 2.1 billion birds on
521 migration. Oikos 118, 624–626

522 Hansen (1954): Birds killed at lights in Denmark 1886-1939. Vidensk Medd den naturhist Foren i København
523 116: 269-368

524 Heim, W, Smirenski, SM (2013) The Amur bird project at Muraviovka Park in Far East Russia. BirdingASIA 31–33

525 Heim, W, Smirenski, SM, Siegmund, A, Eidam, F (2012) Results of an autumnal bird ringing project at
526 Muraviovka Park (Amur Region) in 2011.

527 Heim, W, Pedersen, L, Heim, R, Kamp, J, Smirenski, SM, Thomas, A, Tøttrup, AP, Thorup, K (2018a) Full annual
528 cycle tracking of a small songbird, the Siberian Rubythroat *Calliope calliope*, along the East Asian flyway. J.
529 Ornithol. 159:893–899

530 Heim, W, Eccard, JA, Bairlein, F (2018b) Migration phenology determines niche use of East Asian buntings
531 (Emberizidae) during stopover. Curr. Zool. 64: 681-692

532 Higuchi, H (2012) Bird migration and the conservation of the global environment. J. Ornithol. 153:3–14

533 Higuchi, H, Pierre, JP, Krever, V, Andronov, V, Fujita, G, Ozaki, K, Goroshko, O, Ueta, M, Smirensky, S, Mita, N
534 (2004) Using a Remote Technology in Conservation: Satellite Tracking White-Naped Cranes in Russia and Asia.
535 Conserv. Biol. 18:136–147

536 Kaiser, A (1993) A new multi-category classification of subcoutaneous fat deposits of songbirds. Journal of Field
537 Ornithology 64:246–255

538 Kalnay, E, Kanamitsu, M, Kistler, R, Collins, W, Deaven, D, Gandin, L, Iredell, M, Saha, S, White, G, Woollen, J, et
539 al (1996) The NCEP/NCAR 40-Year Reanalysis Project. Bull. Am. Meteorol. Soc. 77:437–472

540 Kamp, J, Oppel, S, Ananin, AA, Durnev, YA, Gashev, SN, Hölzel, N, Mishchenko, AL, Pessa, J, Smirenski, SM,
541 Strelnikov, EG, et al (2015) Global population collapse in a superabundant migratory bird and illegal trapping in
542 China: Population Collapse in Migratory Bird. Conserv. Biol. 29:1684–1694

543 Kemp, MU, Shamoun-Baranes, J, van Loon, EE, McLaren, JD, Dokter, AM, Bouten, W (2012a) Quantifying flow-
544 assistance and implications for movement research. J. Theor. Biol. 308:56–67

545 Kemp, MU, Emiel van Loon, E, Shamoun-Baranes, J, Bouten, W (2012b) RNCEP: global weather and climate data
546 at your fingertips: RNCEP. Methods Ecol. Evol. 3:65–70

547 Kirby, JS, Stattersfield, AJ, Butchart, SHM, Evans, MI, Grimmett, RFA, Jones, VR, O'Sullivan, J, Tucker, GM,
548 Newton, I (2008) Key conservation issues for migratory land- and waterbird species on the world's major
549 flyways. Bird Conserv. Int. 18:49–73

550 Koike, S, Hijikata, N, Higuchi, H (2016) Migration and Wintering of Chestnut-Cheeked Starlings *Agropsar
551 philippensis*. Ornithol. Sci. 15:63–74

552 Korner-Nievergelt, F, Roth, T, von Felten, S, Guelat, J, Almasi, B, Korner-Nievergelt, P (2015) Bayesian Data
553 Analysis in Ecology Using Linear Models with R, BUGS, and Stan (Elsevier)

554 Labocha, MK, Hayes, JP (2012) Morphometric indices of body condition in birds: a review. J. Ornithol. 153:1–22

555 Leliukhina, E, Valchuk, O (2012) Features of the autumn migration of Yellow-browed warbler (*Phylloscopus*
556 *inornatus*) in the South Primorye (according to the banding data) In: Proceedings of the IV. Conference on
557 Problems of Current Biology, (Vladivostok), 39–49

558 Liechti, F (2006) Birds: blown' by the wind? J. Ornithol. 147:202–211

559 Liechti, F, Bauer, S, Dhanjal-Adams, KL, Emmenegger, T, Zehtindjiev, P, Hahn, S (2018) Miniaturized multi-
560 sensor loggers provide new insight into year-round flight behaviour of small trans-Sahara avian migrants. Mov.
561 Ecol. 6:19

562 Lindström, A, Alerstam, T (1992) Optimal Fat Loads in Migrating Birds: A Test of the Time-Minimization
563 Hypothesis. Am. Nat. 140:477–491

564 Mateos-Rodríguez, M, Liechti, F (2012) How do diurnal long-distance migrants select flight altitude in relation
565 to wind? Behav. Ecol. 23:403–409

566 McKinnon, EA, Love, OP (2018) Ten years tracking the migrations of small landbirds: Lessons learned in the
567 golden age of bio-logging. The Auk 135:834–856

568 Moore, FR, Aborn, DA (1996) Time of Departure by Summer Tanagers (*Piranga rubra*) from a Stopover Site
569 Following Spring Trans-Gulf Migration. The Auk 113:949–952

570 Müller, F, Taylor, PD, Sjöberg, S, Muheim, R, Tsvey, A, Mackenzie, SA, Schmaljohann, H (2016) Towards a
571 conceptual framework for explaining variation in nocturnal departure time of songbird migrants. Mov. Ecol. 4
572 (24):1–12

573 Müller, F, Rüppel, G, Schmaljohann, H (2018) Does the length of the night affect the timing of nocturnal
574 departures in a migratory songbird? Anim. Behav. 141:183–194

575 Nam, H-Y, Choi, C-Y, Park, J-G, Hong, G-P, Won, I-J, Kim, S-J, Bing, G-C, Chae, H-Y (2011) Protandrous migration
576 and variation in morphological characters in Emberiza buntings at an East Asian stopover site. Ibis 153:494–501

577 Newton, I, Brockie, K, Newton, I (2008) The migration ecology of birds. Amsterdam, London. Elsevier-Academic
578 Press

579 R Core Team R: A language and environment for statistical computing. Vienna: R Foundation for Statistical
580 Computing

581 Reid, TA, Tuck, GN, Hindell, MA, Thalmann, S, Phillips, RA, Wilcox, C (2013) Nonbreeding distribution of flesh-
582 footed shearwaters and the for overlap with north Pacific fisheries. Biol. Conserv. 166:3–10

583 Sander, MM, Eccard, JA, Heim, W (2017) Flight range estimation of migrant Yellow-browed Warblers
584 *Phylloscopus inornatus* on the East Asian Flyway. Bird Study 64:569–572

585 Schaub, M, Jenni, L (2001) Variation of fuelling rates among sites, days and individuals in migrating passerine
586 birds. Funct. Ecol. 15:584–594

587 Schmaljohann, H, Eikenaar, C (2017) How do energy stores and changes in these affect departure decisions by
588 migratory birds? A critical view on stopover ecology studies and some future perspectives. J. Comp. Physiol. A
589 203:411–429

590 Schmaljohann, H, Liechti, F, Bruderer, B (2009) Trans-Sahara migrants select flight altitudes to minimize energy
591 costs rather than water loss. Behav. Ecol. Sociobiol. 63:1609–1619

592 Schmaljohann, H, Becker, PJJ, Karaardic, H, Liechti, F, Naef-Daenzer, B, Grande, C (2011) Nocturnal exploratory
593 flights, departure time, and direction in a migratory songbird. J. Ornithol. 152:439–452

594   Schmaljohann, H, Fox, JW, Bairlein, F (2012) Phenotypic response to environmental cues, orientation and
595   migration costs in songbirds flying halfway around the world. Anim. Behav. 84:623–640

596   Schmaljohann, H, Lisovski, S, Bairlein, F (2017) Flexible reaction norms to environmental variables along the
597   migration route and the significance of stopover duration for total speed of migration in a songbird migrant.
598   Front. Zool. 14:17

599   Senda, M, Deguchi, T, Komeda, S, Shigeta, Y, Sato, F, Yoshiyasu, K, Nakamura, N, Tomita, N, Ozaki, K (2018)
600   Increasing the number of captured migrant buntings at an autumn stopover site using sound lures. Ornithol.
601   Sci. 17:103–108

602   Shamoun-Baranes, J, Liechti, F, Vansteelant, WMG (2017) Atmospheric conditions create freeways, detours and
603   tailbacks for migrating birds. J. Comp. Physiol. A 203:509–529

604   Shimazaki, H, Tamura, M, Higuchi, H (2004) Migration routes and important stopover sites of endangered
605   oriental white storks (Ciconia boyciana) as revealed by satellite tracking. 17

606   Stêpniewska, K, Zehtindjiev, P, Ilieva, M, Hnatyna, O (2018) Fuelling strategies differ among juvenile Sedge and
607   Reed Warblers along the eastern European flyway during autumn migration. 95:15

608   Svensson, L (1992) Identification guide to European passerines. 4th ed. Naturhistoriska Riksmuseet, Stockholm:
609   British Trust for Ornithology. (Naturhistoriska Riksmuseet: British Trust for Ornithology)

610   Takekawa, JY, Newman, SH, Xiao, X, Prosser, DJ, Spragens, KA, Palm, EC, Yan, B, Li, T, Lei, F, Zhao, D, et al.
611   (2010) Migration of Waterfowl in the East Asian Flyway and Spatial Relationship to HPAI H5N1 Outbreaks.
612   AVIAN Dis. 54:466–476

613   Valchuk, O, Yuasa, S, and Morosova, E (2005). Migration of Rustic Bunting Emberiza rustica at the eastern edge
614   of Asia. Alauda 73, 323.

615   Wang et al. (2019): Patterns of bird nocturnal migration at Shenyang Taoxian International Airport, Northeast
616   China. Chinese Journal of Applied Ecology 30(1): 292-300. doi: 10.13287/j.1001-9332.201901.013

617   Wang, Y, Chang, J, Moore, FR, Su, L, Cui, L, Yang, X (2006) Stopover ecology of Red-flanked Bush Robin (*Tarsiger*
618   *cyanurus*) at Maoershan, Northeast China. Acta Ecol. Sin. 26:638–646

619   Wikelski, M, Tarlow, EM, Raim, A, Diehl, RH, Larkin, RP, Visser, GH (2003) Costs of migration in free-flying
620   songbirds: Avian metabolism. Nature 423:704–704

621   Yamaura, Y, Schmaljohann, H, Lisovski, S, Senzaki, M, Kawamura, K, Fujimaki, Y, Nakamura, F (2017) Tracking
622   the Stejneger's stonechat *Saxicola stejnegeri* along the East Asian-Australian Flyway from Japan via China to
623   southeast Asia. J. Avian Biol. 48:197–202

624   Yong, DL, Liu, Y, Low, BW, Española, CP, Choi, C-Y, Kawakami, K (2015) Migratory songbirds in the East Asian-
625   Australasian Flyway: a review from a conservation perspective. Bird Conserv. Int. 25:1–37

626   Yong, W, Finch, DM, Moore, FR, Kelly, JF (1998) Stopover Ecology and Habitat Use of Migratory Wilson's
627   Warblers. The Auk 115:829–842

628

629

630

631   Figures

632   Fig. 1: Estimated average energy stores of each species (sample sizes are given above species abbreviation) with 95%

633   credible intervals. Dotted lines indicate which species differ significantly in their energy stores from each other.

634   Abbreviations: tbw – Two-barred Warbler, bbrw – Black-browed Reed Warbler, thbw – Thick-billed Warbler, ybw – Yellow-

635   browed Warbler, rw – Radde's Warbler, pgw – Pallas's Grasshopper Warbler, dw – Dusky Warbler, pllw – Pale-legged Leaf

636   Warbler, aw – Arctic Warbler, plw – Pallas's Leaf Warbler.

637   Fig. 2: Increase in energy stores with hours after sunrise by "first-traps-by-time-of-day-method" modelled with linear mixed

638   effect models separately for each species, the feasibility of this approach is addressed in the discussion and see also

639   Delingat et al. (2009). Species-specific regressions are given as the black solid line and the corresponding 95% credible

640   intervals are given in grey, when the effect was significant. Results of the appropriate linear mixed effect models are

641   provided in Tab. 1.

642   Fig. 3: Increase in energy stores within the season (day of the year) modelled with linear mixed effect models for each

643   species. Species-specific regressions are given as the black solid line and the corresponding 95% credible intervals are given

644   in grey, when the effect was significant. Results of the appropriate linear mixed effect models are provided in Tab. 2.

645   Fig. 4: Estimated flight ranges of each species. Boxplots show the 5, 25, 50, 75 and 95 % percentiles as well as outliers

646   (dots). Significant differences between the groups are graphically illustrated by the non-overlapping "notches". Grey line

647   shows the maximal distance (470 km) birds could cover during one migratory flight bout (with average length of night: 11

648   hours, for details see methods). For abbreviations see Fig. 1.

24