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

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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.

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**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

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

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

239     *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

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

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

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

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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.