

1 Seasonal contrasts in individual consistency of oriental honey buzzards' migration

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13 **KEYWORDS**

14 migration; individual variation; consistency; foraging; *Pernis ptilorhynchus*; satellite tracking

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17 ABSTRACT

18 Individual consistency in migration can shine light on the mechanisms of migration. Most
19 studies reported that birds are more consistent in the timing than in the routes or stopover
20 sites during migration, but some specialist species showed the opposite patterns, being more
21 consistent in spatial than temporal aspects of migration. One possible explanation for this
22 contrast is that specialists rely on particular food or habitat resources, which restrict the
23 migratory routes they can take, leading to high spatial consistency. If this is the case, the
24 effect of specialist foraging should become apparent only when birds forage, instead of
25 fasting and flying continuously. To test this effect, we analysed individual consistency in
26 migration of the oriental honey buzzard (*Pernis ptilorhynchus*), a specialist raptor that feeds
27 on honeybees and wasps, using a long-term tracking data set. As honey buzzards make
28 extended stopovers during which they forage in spring but not in autumn, the spatial
29 consistency should be higher in spring than in autumn. Honey buzzards were highly
30 consistent in both their migratory routes and stopover sites in Southeast Asia, but only during
31 spring migration. Our results highlight an important link between species' migratory
32 consistency and foraging ecology.

33

34 INTRODUCTION

35 Individual consistency, or how repeatable individual animals are, in various aspects of
36 migration (e.g., [1–9]) helps unveiling the mechanisms of long-distance migration. As
37 different mechanisms would result in varying patterns in migratory consistency, individual
38 histories of migration would help interpreting the roles of genetic variation and learning in
39 shaping these patterns [2,10,11].

40 Most studies reporting the repeatability of migration found that birds are more
41 repeatable in timing their migration than in their routes or stopovers (e.g., [3,4,6,7]). There

42 were, however, a couple of exceptions including ospreys (*Pandion haliaetus*; [8]) and great
43 reed warblers (*Acrocephalus arundinaceus*; [9]), both specialists relying on a particular prey
44 or habitat (respectively, fish and reed beds). These two species were more repeatable in the
45 routes and stopover sites than in the timing of migration. It has been suggested that one
46 reason why these birds were more consistent spatially than temporally is that they have to
47 travel through a specific type of habitat that may be scarce but widespread [8,9]. If this is the
48 case, however, this pattern should only hold when birds forage, and not when they fast and
49 travel non-stop to their destinations.

50 That specialist foraging constrains migration routes agrees to the emerging consensus
51 that foraging is intimately linked to various aspects of migration [12,13]. To address this link,
52 we investigated the spatial and temporal consistency of migration in the oriental honey
53 buzzard (*Pernis ptilorhynchus*), a specialist raptor foraging on honeybees and wasps, using a
54 long-term tracking data set. Oriental honey buzzards that breed in Japan migrate through East
55 and Southeast Asia to spend winter in the Malay archipelago [14,15]. Honey buzzards rarely
56 stopover during their autumn migration, but in spring, make stopovers that can last for weeks
57 before reaching the Korean Peninsula [14,15]. This asymmetry in stopovers between the
58 autumn and spring migration provides an opportunity to test how foraging specialism affects
59 the consistency of the migratory route. If specialist species, such as the honey buzzard, are
60 constrained in their migratory routes and stopovers by their foraging requirements, then the
61 spatial aspects of honey buzzard migration, such as the migratory route, should be more
62 consistent in spring than in autumn. In addition, within the spring migrations, the degree of
63 spatial consistency should be more pronounced around the stopover sites, in which birds are
64 considered to forage for extended periods. To test these hypotheses, we examined whether
65 the honey buzzard, a specialist feeder, is more consistent in spatial aspects in spring than in
66 autumn, and if so, whether the high consistency corresponds with birds' stopover sites.

67 MATERIAL AND METHODS

68 *Tracking data set*

69 To estimate individual consistency, we used long-term tracking data from 30 wild oriental
70 honey buzzards (11 females; 19 males; all adults) with at least two journeys in the same
71 season (autumn/spring). Each bird was tagged with a satellite transmitter (Solar Argos by
72 North Star Science and Technology, LLC; Solar Argos or Solar Argos/GPS by Microwave
73 Telemetry, Inc.) using harnesses with Teflon ribbons (for technical details, see [14]). Each
74 tag plus harness weighed between 9.5–30g (0.7–3.2% of the bird's body weight), and was
75 tracked by the Argos system in Toulouse, France [16]. To exclude off-track data points, we
76 processed the Argos data using the Douglas Argos filter [17]. The locations of 11 out of 30
77 tags were also calculated by the GPS (errors: $\pm 18\text{m}$ [18]). For these, we used only the high-
78 quality GPS-based location data for the analyses, as GPS and Argos data from the same birds
79 showed similar results for crossing (see below), but GPS offered more frequent data points
80 (mean sampling intervals for GPS and Argos: 5.17 and 14.55 h).

81

82 *Identifying longitudes and dates of latitude crossings*

83 To calculate temporal and spatial consistency in migration, we identified the dates and
84 longitudes on which the birds crossed the latitudes 0, 5, 10, 15, 20, 25 and 30°N [3]. This
85 area encompasses three major regions the honey buzzards travel through in both autumn and
86 spring: the Malay Peninsula, Southeast Asia and Mainland China (Fig. 1). This area was
87 chosen for data analyses to include data from as many individuals as possible, regardless of
88 differences in their breeding/wintering sites and the seasonal difference in migratory routes.
89 As for the crossings of 0, 5 and 10°N, we only included those that occurred on southern
90 Thailand, the Malay Peninsula or Sumatra area, excluding crossings on Borneo and the
91 Philippines on the way to different wintering grounds (Fig. 1). When birds crossed the focal

92 latitude multiple times within the same season as they meandered in the area, we used the last
93 crossing (i.e., when birds actually left the relevant area) for the analyses. To estimate the
94 repeatability, we included birds that had two or more data points for crossing each latitude.
95 As there were cases where the data points immediately before and after the latitude crossing
96 were weeks apart, we excluded cases in which two data points before and after the crossing
97 were more than 72 hours apart, based on data distribution (for the sample size, see Fig. 2).

98

99 *Identifying stopovers*

100 To estimate consistency in honey buzzards' stopovers, we defined stopovers as days on
101 which birds travelled less than 50 km between 0-30°N for longer than 7 days. To calculate
102 daily travel distance, we chose a single data point per day with the best location accuracy and
103 the earliest sampling time. We then calculated time difference and distance between two
104 neighbouring points on the WGS84 ellipsoid, using the 'difftime()' function and the
105 'distGeo()' function in the 'geosphere' package [19]. The daily travel speed was calculated
106 by dividing the distance by the time difference. When there were days on which no location
107 data were available during a stopover, the two points before and after those days were
108 considered to belong to the same stopover if the distance between the two was less than 50
109 km. We included birds that had stopover data for two or more years into the subsequent
110 analyses. Six out of 62 cases were additional stopovers by four birds: they had two stopovers,
111 one in the area they stayed in other years, and another in a distinct area, within the same year
112 (Supplementary material 1). For these, we used the stopovers in the area used in other years.

113

114 *Consistency in latitude crossings and stopovers*

115 To quantify consistency in the latitude crossings and the stopovers, we first converted the
116 dates of crossings and stopovers into Julian days (i.e., 1 January = 1). We then estimated and

117 tested the significance of individual consistency (at $\alpha = 0.05$), in either: the Julian day or the
118 longitude of the latitude crossings, the arrival/departure Julian day of the stopovers, or the
119 latitude/longitude of the centroids of the stopover sites, using the 'rpt()' function in the 'rptR'
120 package [20]. We used R [21] for all data analyses. Data for latitude crossings and stopovers
121 are available via Dryad [22].

122

123 RESULTS

124 *Consistency in longitudes and dates of latitude crossings*

125 The most repeatable sections of the migration, in terms of the difference in longitude between
126 years, differed between the spring and autumn migrations. The spring migration showed high
127 repeatability at higher latitudes, peaking around 15-25°N, while the repeatability of the
128 autumn migration became higher at lower latitudes close to their wintering grounds (Fig. 2a).
129 The timing of the migration was significantly repeatable at all latitudes across years within
130 each season (Fig. 2b). The timing of the spring migration appeared to be slightly more
131 repeatable than that of the autumn migration, in particular at 20°N, but the differences were
132 not as distinctive as in the repeatability estimates for longitudes.

133

134 *Consistency in stopover sites*

135 The honey buzzards almost exclusively made substantial stopovers during the spring migration
136 (61 out of 62 stopovers; Supplementary material 1). The locations of these stopovers were
137 exceptionally repeatable (Fig. 2c), showing that birds precisely returned to specific sites year
138 after year. Individual stopover sites were spread between 8.59–23.69°N (mean \pm SD: 17.13 \pm
139 4.61°N), centring on the most repeatable sections of the spring migration (15–20°N; Fig. 2a).
140 The timing of stopovers was also significantly repeatable (Fig. 2c), spanning between February
141 to May (one stopover in October was excluded from the analyses; Supplementary material 1).

142

143 DISCUSSION

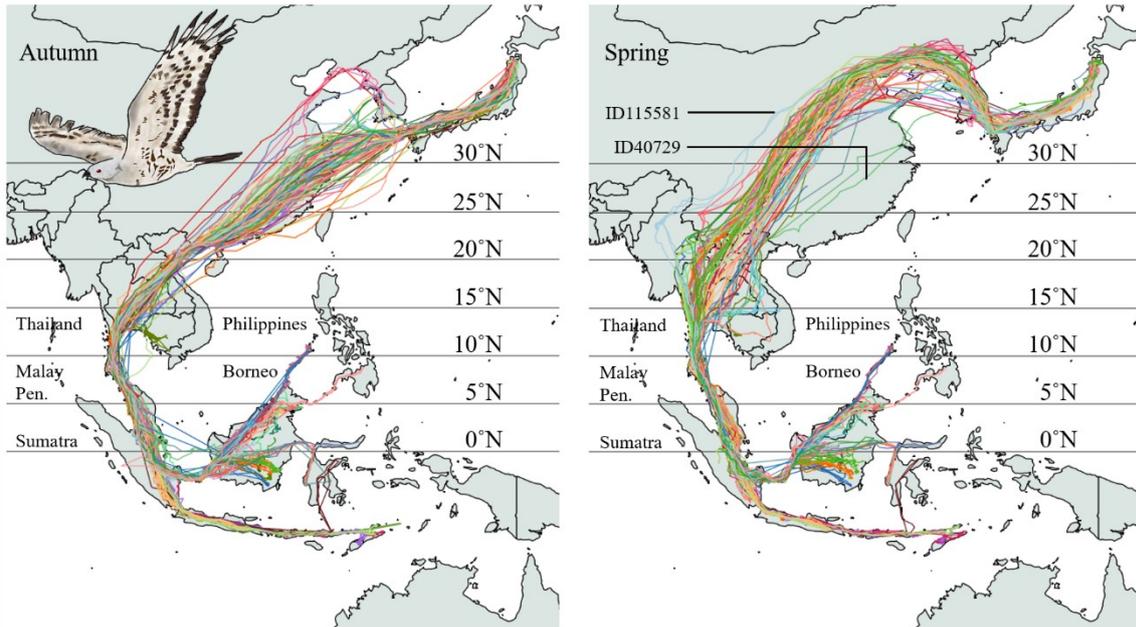
144 The most repeatable sections of oriental honey buzzards' migratory routes differed between
145 seasons, with the spring migration being most consistent across years around 15-25°N in
146 Southeast Asia, whereas the autumn migration was most consistent around 0-5°N in the Malay
147 archipelago. Honey buzzards made long stopovers almost exclusively in spring. The locations
148 of stopover sites spread across Southeast Asia, and were exceptionally consistent between years.
149 Despite these differences in the repeatability of routes between seasons, the consistency in
150 timing of migration did not show clear seasonal differences. The dates on which birds crossed
151 different latitudes was repeatable across all regions within season. The arrival/departure dates
152 of stopovers were also significantly repeatable.

153 Similar to other specialist species [8,9], oriental honey buzzards were more consistent
154 in the routes and stopovers, than in the timing of their migration, but only in spring (Fig. 2).
155 This could be because of various factors. The lower repeatability in the early part of the autumn
156 migration route may be due to ocean crossing. In autumn, honey buzzards cross the 650-km-
157 wide East China Sea (Fig. 1) in strong tail winds [23]. While crossing the ocean, birds may be
158 susceptible to stochastically-changing wind directions, and have no landscape features that they
159 can use to follow specific routes. This combination of wind conditions and the lack of
160 landmarks on the ocean may together decrease spatial consistency in higher latitudes in autumn.
161 At lower latitudes, in autumn as well as in spring, birds do not cross any large barrier (Fig. 1;
162 [14]), and thus can land at any time and wait for better wind conditions. This may give birds
163 better control over where they go, resulting in higher consistency.

164 The high spatial repeatability in Southeast Asia in spring may be due to highly
165 consistent spring stopovers in the area. Honey buzzards select stopover sites that contain
166 suitable features for local honeybees including the giant honeybee (*Apis dorsata*; [24, 25]).

167 While the high repeatability implies the general stability of local prey abundance in the
168 stopover sites, interestingly, birds retained some degree of flexibility in stopovers, as birds
169 made multiple stopovers in handful of cases (Supplementary material 1). This could be due to
170 birds responding to fluctuating food resources and competition with conspecifics. For instance,
171 when birds made multiple stopovers within a migratory trip, each stop was shorter than the
172 same bird's single stopover in other years (Supplementary material 1), suggesting that birds
173 made the second stopovers seeking for additional foraging opportunities. This flexibility,
174 together with the high repeatability of individuals' stopover sites, suggests that honey buzzards
175 might learn the precise location of the stopover sites, although further behavioural and
176 environmental data are needed to understand the mechanisms involved in site selection.

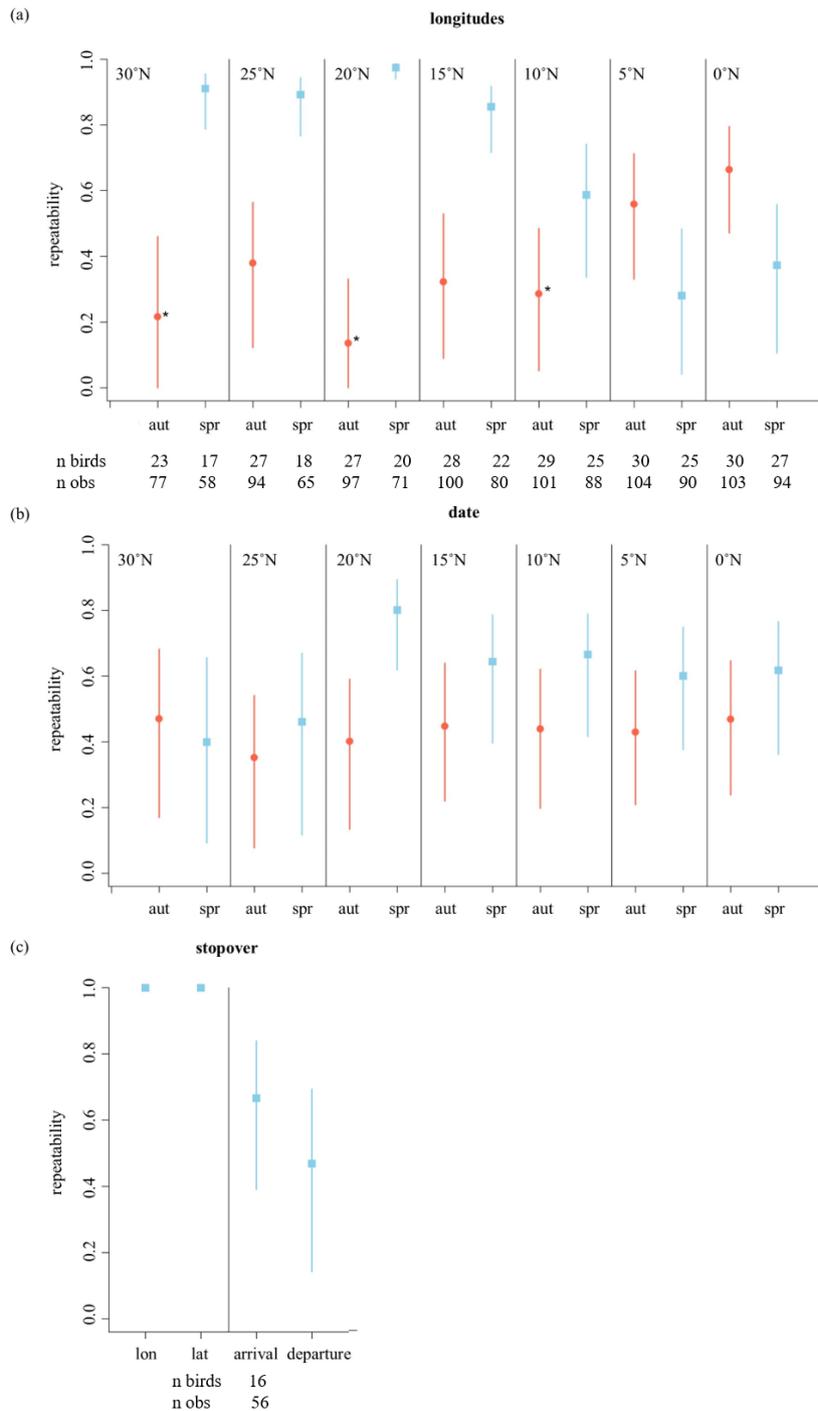
177 Feeding specialists including oriental honey buzzards may rely on resources that might
178 emerge in specific environments at specific timing during migration [26], unlike generalists.
179 Thus in prenuptial migration, specialists not only need to arrive at breeding sites on time, but
180 have to meet their requirement to forage on specific resources. These differences may lead to
181 differences in developmental processes of migration between specialists and generalists.
182 Specialists, for instance, may establish their highly consistent stopover sites early in life, by
183 exploring and finding a productive site, and later refine the migratory route to the site through
184 learning [2]. On the other hand, generalist migrants like black kites (*Milvus migrans*) might be
185 less restricted to specific routes and stopover sites, but need to develop other abilities to time
186 their departure appropriately, or to respond to weather conditions [7]. Large-scale datasets have
187 started producing important insights into the effects of foraging ecology on migration,
188 elucidating the mechanisms of migration [12], and demonstrating the resilience of migrant
189 species [13]. To further our understanding of this link between foraging and movement ecology
190 in migrants, it is crucial to gather long-term data about behaviour, and about spatial distribution
191 of food across migratory routes.



193

194 Figure 1. Oriental honey buzzards' migratory routes in autumn and spring. Different colours
195 indicate migratory routes by individuals. See supplementary material 2 for details of migration
196 by ID115581 and 40729.

197



198

199 Figure 2. Repeatability (r) estimates (Supplementary material 3) of: (a) longitudes and (b)
 200 dates on which birds crossed 30, 25, 20, 15, 10, 5 and 0°N during autumn (aut) and spring (spr)
 201 migrations, and (c) longitudes and latitudes of centroid of stopover sites, and arrival and
 202 departure dates of stopovers. Bars show 95% confidence interval. Asterisks indicate non-
 203 significant repeatabilities.

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285

286 AUTHOR CONTRIBUTIONS

287 S.S. designed and carried out the analyses, and drafted the manuscript. H.H. provided the data,
288 helped designing and interpreting the analyses, and edited the manuscript. All authors agree to
289 be held accountable for the content therein and approve the final version of the manuscript.

290

291 DATA ACCESIBILITY

292 Input data and R scripts: <https://datadryad.org/review?doi=doi:10.5061/dryad.1g1hh58>

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294

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298

299 COMPETING INTERESTS

300 We have no competing interests.

301

302 ETHICAL STATEMENT

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305