The large-scale detoured migration route and the shifting pattern of migration in Oriental honey-buzzards breeding in Japan


1 Laboratory of Biodiversity Science, School of Agriculture and Life Sciences, The University of Tokyo, Tokyo, Japan
2 Abiko City Museum of Birds, Chiba, Japan
3 Shinshu Raptor Migration Research Group, Nagano, Japan
4 Satoyama Natural History Research Group, Chiba, Japan
5 Nagano Environmental Conservation Research Institute, Nagano, Japan
6 Raptor Conservation Center, The Ministry of the Environment, Yamagata, Japan
7 Faculty of Education, Shinsu University, Nagano, Japan

Keywords
detoured migration; oriental honey-buzzard; Pernis ptilorhyncus; satellite-tracking.

Abstract
We describe the detoured migration route of the Oriental honey-buzzard Pernis ptilorhyncus, showing differences between autumn and spring migration, using data from 10 adult individuals marked with satellite transmitters. In autumn, the migration routes were very similar from Japan to the south end of the Malay Peninsula. The wintering sites were distributed within the Philippines, Borneo and the Malay Archipelago. During autumn, migration of the birds had few long-term stopover sites, instead, sometimes decidedly slowing their migration rate while proceeding in a consistent direction. During spring migration, the honey-buzzards penetrated into southern China, moving north to the base of the Korean Peninsula. The birds then went south through the Korean Peninsula to reach Japan. Before travelling to China, all spring migrants stopped for several weeks in southeast Asia. The slow rate of travel in the autumn suggests that migrants were foraging and replenishing their energy reserves. Instead of a migration strategy that uses only a few long-term stopover sites, honey-buzzards may adopt a strategy based on a number of short-term stay sites.

Introduction
Satellite tracking is a powerful tool for investigating animal movements, in particular when a subject travels on a global scale (Cohn, 1999; Webster et al., 2002). Using this technology, ecologists have accumulated evidence concerning migratory pathways, stopover sites (e.g. Higuchi et al., 1996; Green et al., 2002; Hake, Kjellén & Alerstam, 2003) and foraging ranges (Brothers et al., 1998). These studies have not only provided basic information on the movements of a target species but also contributed to the conservation of species by indicating important stopover sites or areas of overlap between foraging birds and longline fisheries (Brothers et al., 1998; Higuchi et al., 2004).

In general, satellite tracking alone merely provides time and location data (when and where an animal occurs). However, by integrating such data with dietary information on a tracked species, or GIS information such as the geographical characteristics (wetlands, grassland, forests and so on) of a location, some researchers have examined strategies of migration (e.g. Thorup et al., 2003; Fujita et al., 2004) and inter-specific competition for food resources (Barlow et al., 2002). Moreover, migrations can be characterized from the spatio-temporal patterns of movement speed and direction calculated from satellite tracking data. These detailed analyses have the potential to reveal the adaptive significance of a migration route and the evolution of migratory behaviour.

The Oriental honey-buzzard Pernis ptilorhyncus, which breeds in southern Siberia, northern Mongolia, northeastern China, Korea and Japan, and migrates south for winter (Ornithological Society of Japan, 2000), is a suitable and attractive subject for studying behavioural and evolutionary ecology of migration in birds for the following reasons: (1) the species is large enough to carry a satellite transmitter; (2) earlier satellite tracking studies have shown that this species migrates very long distances, almost 10 000 km, and that at least some individuals exhibit a quite unique migration in...
which the birds use a largely detoured route between nesting and wintering areas (Higuchi et al., 2005; Shiu et al., 2006); (3) Oriental honey-buzzards are congenic with the European honey-buzzard *Pernis apivorus*, which is one of the most investigated species of migrating raptors in Europe (e.g. Agostini & Logozzo, 1995; Hake et al., 2003; Agostini et al., 2005). Previous studies showed that European honey-buzzards followed a detoured autumn migration route between Sweden and western Africa, with the routes used to cross the Mediterranean Sea differing between autumn and spring. The opportunity exists to compare and contrast the evolution of detoured migration routes in these two closely related species.

Here, we describe both autumn and spring migration routes of Oriental honey-buzzards using data from 10 satellite-tracked adult individuals, belonging to the population breeding in Japan, to confirm that large-scale detoured migration is a common characteristic of the species. We also show individual differences in migratory behaviour because the results of Higuchi et al. (2005) and Shiu et al. (2006) are from only two adults and one juvenile. In addition, we characterize the autumn and spring migration strategy of the Oriental honey-buzzard by analysing movement speed. From the analysis, we propose a novel hypothesis to explain why honey-buzzards follow large-scale detoured routes during migration.

**Methods**

**Satellite tracking**

We captured an adult female (ID: 41317) and an adult male (ID: 41313) in Azumino (36°06′N, 130°40′E) and Shirakaba-toge (36°06′N, 137°40′E), Nagano Prefecture, Japan, on 6 July and 15 September 2003, respectively. In 2006, three males (IDs: 66547–66549) were captured in Okitama, Yamagata Prefecture, Japan (37°55′, 139°54′E), on 17 July, and two males and three females (male IDs: 66550 and 66552; female IDs: 66551, 66553 and 66554) in Shiojiri, Nagano Prefecture, Japan (36°06′N, 137°59′E), on 17 July. Azumino, Okitama and Shiojiri were the breeding sites of the captured birds. Shirakaba-toge is a hilltop concentration of migrating honey-buzzards. We captured these birds harmlessly using flat spring net traps. The traps were placed on the ground and birds were attracted to the traps by honeycomb baits. The captured birds (41313, 41317, 66547–66554) weighed 1400, 1150, 1050, 1020, 1100, 974, 995, 1027, 1307 and 1000 g, respectively, at the time of capture. Each trapping process (from when the traps were set to when a bird was captured) took about an hour. It took c. 30 min to deploy a PTT and measure some morphological traits (body weight, wing length, etc.).

Satellite transmitters (platform transmitter terminals [PTTs], Model 16GS by North Star Science and Technology) were deployed to the back of the birds with a harness system. The harness consisted of two Teflon-treated ribbons, which were attached by sewing to each of the two anterior corners of the PTT. Ribbons met at the keel of the bird’s sternum, where they crossed and passed through a small tube and were sewn together with a nylon thread. The ribbons were attached by sewing to each of the two posterior corners of the PTT. We expected the PTTs to fall off when the thread deteriorated 2–3 years after the attachment. These solar-powered PTTs weighed 20 g, and were 50 × 20 × 17 mm in size with an antenna length of 198 mm. The weight of a PTT plus harness materials was equivalent to only 1.4–2.1% of the body mass of the birds.

The PTT locations were estimated by the Argos system (Argos, 1996). The estimated locations were reported as latitude and longitude (WGS84), with measurement times recorded as Greenwich Meridian Time. Argos classified the location accuracy (location class, LC) into 3, 2, 1, 0, A, B and Z. The standard deviations of positional error in latitudinal and longitudinal axes were <150 m for LC 3, between 150 and 350 m for LC 2, between 350 and 1000 m for LC 1 and >1000 m for LC 0. The location accuracy for LCs A, B and Z was not specified by Argos. Because other studies have reported that the accuracy of LC 0 is approximately within 10 km (Brothers et al., 1998; Britten, Kennedy & Ambrose, 1999; Hays et al., 2001), the standard deviation may be <5 km for LC 0. In this study, we assumed the standard deviation of positional error in latitudinal and longitudinal axes to be 150 m for LC 3, 350 m for LC 2, 1000 m for LC 1 and 5 km for LC 0.

We used locations of LCs 0–3 to draw autumn migration routes, but used locations of A, B and 0–3 to draw spring migration, because only 6–15% of all locations obtained were determined as LCs 1–3, 40–60% were LC 0 and the accuracy level of locations were mostly quite low for the spring migration. We think the LC 0, A and B locations can be used in the analysis because Oriental honey-buzzards move thousands of kilometres during migration and some location errors can be neglected at such a spatial scale.

We defined a stopover site as ‘an area where a honey-buzzard did not travel in one particular direction (i.e. they exhibited a more or less random movement pattern) for at least 24 h’. A wintering site was defined as ‘the site from which the bird exhibited directional movement to a breeding site (i.e. spring migration)’. If a PTT location had no adjacent location for more than 24 h, we did not classify it as a stopover site, because we could not distinguish between a bird actually staying at a single location and signals being scarce around the location.

**Calculation of travel distance and speed**

The travel distance from one site to the next was calculated as the geodesic distance between two coordinates on the ellipsoid, using Vincenty’s inverse formulae (Vincenty, 1975). The travel speed between the two points was calculated by dividing the travel distance by the intervening time interval between the points. To determine the migration state (see the next section) of a honey-buzzard *i* at a location interval *j*, we calculated daytime travel speeds *v*(i,j) (km day−1). An interval *j* was defined as the interval from an arbitrary location *j*start to the nearest point to *j*end among the points recorded between 3 and 12 h from *j*start, and that
satisfied the accuracy criterion defined as the standard deviation of travel speed, $\sigma_v \leq 15$. Daytime was defined as 06:00–18:00 h, local time. When we could not find the appropriate $f_{\text{end}}$ for a point $f_{\text{start}}$, $v(i,j)$ of the interval were not calculated. We followed the method of Shimazaki et al. (2004) when calculating $\sigma_v$.

**Determination of the migration state**

We estimated the migration state of travelling honey-buzzards, based on changes in travel speed. The rule to determine the migration state of a bird $i$ at location interval $j$, $s(i,j)$ was that

- $s(i,j)$ is *travel*, if $v(i,j) - 1.96\sigma_v > T$
- $s(i,j)$ is *stay*, if $v(i,j) - 1.96\sigma_v \leq T$

where $T$ is the 50th percentile of $v(i,j)$ in the breeding and the wintering sites, and the two migration states indicate that a bird is in transit from one stay site to the next (*travel*) or is stationary within a range (*stay*). The 50th percentile was obtained by a bootstrapping method (Efron & Tibshirani, 1998).

We examined whether the proportion of the total distance of *stay* intervals to the total distance of *travel* and *stay* intervals combined differed between the high and the low latitudinal segments of a migration route. To perform such an analysis, we used general linear models in which the dependent variable was the proportion of a total distance of *stay* to a total distance of *stay* and *travel* intervals, the independent variable was the categorical assignment of high or low latitudinal segment, the blocking factor was individual identity and the weight to be used in the fitting process was a total distance of *stay* and *travel* intervals for a bird. A migration route was divided in two segments at the northern circle ($23\,\text{°}26\,\text{N}$), because tropical forests develop in the south from the latitude in Asia (Whitmore, 1998) and habitat conditions for migrating honey-buzzards would change drastically.

**Results**

**Autumn migration**

We successfully tracked 10 adult honey-buzzards during the autumn migration period. The migration routes of the birds were very similar until they reached the south end of the Malay Peninsula (Fig. 1a). After departing from breeding areas in Japan, they migrated west c. 680 km across the East

![Figure 1](image_url)
The birds continued moving from the Malay Peninsula, but the directions and terminal points differed among individuals. After reaching Sumatra, seven birds (41313, 66547, 66549, 66550, 66551, 66552, 66553) changed their travel direction to north-east. Only one individual (41313) arrived in Mindanao, the Philippines through Borneo, and six individuals ended their migration on Borneo Island. The other three (41317, 66548, 66554) moved along the Malay Archipelago and ended their migration at Bankga Island (66548), central Java (41317) and Flores Island (66554), respectively.

We could determine the departure dates from breeding sites for six individuals, and the arrival dates at the wintering sites for eight individuals (Table 1).

Nine honey-buzzards had distinct wintering sites on Mindanao Island (41313), Borneo (66547, 66549, 66550, 66551, 66552 and 66553), Bankga Island (66548), central Java (41317) and Flores Island (66554). However, 66550 did not have any distinct wintering site, although he stopped over in central Borneo for 10 days. After that 10-day stopover, he moved eastwards again and reached eastern Borneo on 6 December (Table 1), but he did not stay there before starting the spring migration (northwestward).

Females tended to both arrive at and depart from their wintering sites earlier than males. However, arrival dates, departure dates and stay durations at the wintering sites differed greatly among individuals (Table 1).

**Migration states and stopover behaviour**

In Fig. 2a, we show migration states (travel and stay) along routes and distinct stopover sites where birds stayed for more than 1 day. During autumn migration, the tracked honey-buzzards had only a few stopover sites, not stopping in any location for any great length of time. Instead, they sometimes travelled in the stay state (i.e. slowed down their migration speed extremely, but continued to move in one direction). This shifting pattern of migration states differed among individuals, although stay states were seldom observed from departure points to around the northern circle and were frequently observed southward from the latitude for all birds. The difference was statistically significant (general linear model, $F_{1,9} = 16.83, P = 0.003$).

Travel speed varied between nearly 0 km day$^{-1}$ and c. 580 km day$^{-1}$ (figures are available at Supplementary Material Appendices S1 and S2). Most birds crossed the East China Sea relatively quickly. Six birds (66547, 66550, 66551, 66552, 66553 and 66554) travelled at relatively high speeds from Japan to southern China, and then slowed down in south-east Asia. The other four birds (41313,
Table 1 Departure dates, arrival dates and total migration days of tracked individuals

<table>
<thead>
<tr>
<th>ID (sex)</th>
<th>Departure date from breeding site</th>
<th>Arrival date at wintering site</th>
<th>Total days of autumn migration</th>
<th>Stay duration at wintering site</th>
<th>Departure date from wintering site</th>
<th>Arrival date at breeding site</th>
<th>Total days of spring migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>41317 (F)</td>
<td>2006.09.13</td>
<td>11.11</td>
<td>59</td>
<td>115</td>
<td>2007.03.06</td>
<td>05.21</td>
<td>76</td>
</tr>
<tr>
<td>66547 (M)</td>
<td>2006.09.09</td>
<td>11.26</td>
<td>78</td>
<td>NAa</td>
<td>NAa</td>
<td>NAa</td>
<td>NAa</td>
</tr>
<tr>
<td>66549 (M)</td>
<td>2006.09.03–09.14</td>
<td>11.09</td>
<td>56–67</td>
<td>127</td>
<td>2007.03.16</td>
<td>05.21</td>
<td>66</td>
</tr>
<tr>
<td>66550 (M)</td>
<td>2006.09.24</td>
<td>NAab</td>
<td>NAab</td>
<td>NAab</td>
<td>2006.12.07</td>
<td>05.21</td>
<td>165</td>
</tr>
<tr>
<td>66551 (F)</td>
<td>2006.09.18</td>
<td>11.06</td>
<td>61</td>
<td>31</td>
<td>2007.02.16</td>
<td>NAe</td>
<td>NAe</td>
</tr>
<tr>
<td>66552 (M)</td>
<td>2006.09.29–10.01</td>
<td>12.17</td>
<td>77–79</td>
<td>61</td>
<td>2007.02.27</td>
<td>05.13</td>
<td>75</td>
</tr>
<tr>
<td>66553 (F)</td>
<td>2006.09.12–09.20</td>
<td>11.09</td>
<td>50–58</td>
<td>110</td>
<td>2007.02.26</td>
<td>NAe</td>
<td>NAe</td>
</tr>
<tr>
<td>66554 (F)</td>
<td>2006.09.17–09.19</td>
<td>11.07</td>
<td>49–51</td>
<td>111</td>
<td>2007.02.26</td>
<td>NAe</td>
<td>NAe</td>
</tr>
</tbody>
</table>

\[a^\text{Signal lost at 7 December 2006.}\]
\[b^\text{66550 did not have a distinct wintering site.}\]
\[c^\text{Signal lost at 14 April 2007.}\]
\[d^\text{Signal lost at 21 May 2007.}\]
\[e^\text{Signal lost 20 May 2007.}\]

41317, 44548, 66549) did not have any clear pattern for changes in their speed of travel.

Spring migration

We tracked nine honey-buzzards during the spring migration period, although signals from 41313 were partially missed and the radio transmission of 66550 ceased at 21.49°N, 97.58°E. During the spring migration period, we could not obtain signals at all from 66548 (Fig. 1b).

From the wintering sites to the end of the Malay Peninsula, the tracked birds mainly followed the same routes used during autumn migration. They travelled northwestward along the Malay Islands and the Malay Peninsula, and then moved to inland China after going north through Thailand, Laos and Vietnam. The routes in inland China were located north of those used during autumn migration, before the birds reached the end of Korean Peninsula. Unlike autumn migration, the birds detoured around the East China Sea by travelling the length of the Korean Peninsula and crossing the Korean/Tsushima Strait to reach Japan.

At least seven birds (41313, 41317, 66547, 66549, 66550, 66551 and 66553) arrived at the sites where they had bred the previous year, and for six of which we were able to detect their arrival dates (Fig. 1b, Table 1). We confirmed the arrival of 66550 at the previous year’s breeding site by recapturing him, although the signal from that bird ceased when we lost him judging from the limited number of signals and their low LCs. All six arrival dates concentrated in late May, but females tended to arrive earlier than males (Table 1).

Migration states and stopping over behaviour

Migration states along the routes are shown in Fig. 2b. Owing to the number of signals received, for all individuals, being small and their location accuracy low, we could not estimate with any great accuracy the migration state of birds when they were between latitudes of 20°N and 40°N. In the estimated intervals, the honey-buzzards had only a few stopover sites and sometimes travelled in the stay state as in autumn migration. The shifting pattern of migration states differed among individuals. However, we found that stay states were hardly observed for intervals north of 23°26’N and were frequently observed lower than that latitude, a situation similar to that of the autumn migration pattern.

The difference between latitudinal categories was statistically significant (general linear model, $F_{1,6} = 8.30, P = 0.028$). We also found that all individuals stopped over for a long time at some sites in south-east Asia before travelling to China. The duration of such stopovers varied from 1 to 5 weeks.

Travel speed ranged from nearly 0 km d$^{-1}$ to c. 490 km d$^{-1}$ (figures are available at Supplementary Material Appendix S1 and S2). The three birds, 41317, 66547 and 66551, for which we could obtain sufficient data, moved at relatively slow speeds from the wintering sites to the stopover sites in south-east Asia, and travelled at higher speeds to the terminal sites after departing the stopover sites in south-east Asia.

Discussion

In this study, we found that adult Oriental honey-buzzards that breed in Japan use very similar migration routes at a large scale, although the routes are largely detoured, and that females arrive at and depart from wintering sites earlier than males. These characteristics were similar to those of European honey-buzzards (Hake et al., 2003). On the other hand, some European honey-buzzards undertake longer sea crossing in spring than in autumn, unlike the Oriental honey-buzzards we tracked (Agostini & Panuccio, 2005). This similarity and dissimilarity in the migration patterns will be studied thoroughly elsewhere in the near future.
In autumn migration, the routes from departure sites to the south end of the Malay Peninsula were very similar among individuals. All birds directly crossed the East China Sea and travelled southwestward in the Asian continent. From the Malay Peninsula, two patterns of migration routes were observed: the route along the Malay Archipelago, and that to Borneo and the Philippines. The terminal points largely differed among individuals despite the birds having originated from only two breeding sites and one concentration point of migrating buzzards. This result indicates that there is no one-to-one relationship between a breeding site and a wintering site in this species, and that birds in the same breeding site may experience different ecological conditions in winter. It seems that neither sex-related nor breeding site-related differences exist between the two patterns of migration, although we could not carry out statistical analyses due to the limited sample sizes.

The duration of stay at the wintering site differed remarkably among individuals, and one individual (66550) lacked a distinct wintering site altogether. It remains unknown why the differences occurred, but the habitat quality, particularly related to food, and a strong competition in the wintering quarters (Agostini & Mellone, 2007) may have an effect on the phenomenon. Local distribution, abundance and spatio-temporal changes in food resources (e.g. colonies of the giant honeybee *Apis dorsata*) and interrelationships among different individuals in the winter season should be examined.

The migration routes in spring differed from those of autumn. The main differences were that (1) all tracked birds took more inland routes in spring than in autumn and detoured around the East China Sea via the Korean Peninsula and (2) all birds stayed at some locations in south-east Asia for 1–5 weeks before entering inland China. Avoiding geographical barriers such as seas, lakes or deserts is a common migration strategy in raptors (e.g. Kerlinger, 1989, 1995), and whether a bird detours or not is affected partly by climatic conditions (Alerstam, 2001). In Oriental honey-buzzards, climatic conditions in the East China Sea may be favourable in autumn, but not in spring, which may have affected the evolution of the migration strategy in this species. In autumn, for example, honey-buzzards could

![Figure 2 Shifting patterns of migration states (travel and stay) of 10 adult honey-buzzards (a) in autumn 2003 (IDs 41313 and 41317) and 2006 (IDs 66547–66554) and (b) in spring 2004 and 2007. Migration intervals in travel and stay states are shown in blue and red, respectively. Small grey dots indicate points with a location accuracy of LC 0–3. Distinct stopover sites where birds stayed for more than 1 day are shown in open square symbols with staying dates. The horizontal solid line indicates the latitude of 23°26’ N, at which the migration data were divided into two segments (see ‘Methods’).](image-url)
cross the East China Sea using the easterly tail winds that occur following passage of a high-pressure system (H. Higuchi & Y. Shimada, unpubl. data). In early to mid-May, when all the tracked birds moved along the Korean Peninsula, the stationary weather front develops over the East China Sea, which causes continuous rain or storms, making a marine passage difficult at that time. By contrast, a northerly tail wind then occurs over the Korean Peninsula, and travelling birds could benefit from such a favourable wind (H. Higuchi & Y. Shimada, unpubl. data). However, during spring migration, Oriental honey-buzzards flew inland without attempting the water crossing and consequently they were not directly affected by weather conditions at the East China Sea (also see Agostini & Mellone, 2007).

Interestingly, a small number of honey-buzzards have been observed to come across the East China Sea to the northwestern coast of Kyushu in late March, about 1.5 months earlier than our satellite-tracked birds (M. Kamogawa, pers. comm.). The weather conditions in March may be favourable for honey-buzzards to cross the East China Sea then. It is not known why there are honey-buzzards arriving in Japan at such an early season when the abundance of honeybee and wasp colonies is low (Ono, 1997; Sugahara, 2005).

Regarding the buzzards’ long stopovers before entering inland China, migratory behaviour may be influenced by both climatic and habitat conditions. If honey-buzzards meet the paucity of suitable foraging habitat or weather conditions forcing long-lasting powered flights without soaring during migration across inland China, they may be required to store considerable energy during one or more long stopovers before entering inland China. Actually, the number of honeybee colonies is limited and colonies of vespid wasps do not grow in the late April of East Asia (Ono, 1997; Sugahara, 2005). These hypotheses are still not beyond a speculation and should be tested in the future using empirical data such as weather conditions.

We estimated migration states (stay or travel) in a migration route using the change in migration speeds and average speed of movements in breeding site and wintering sites. The honey-buzzards sometimes exhibited the stay state during migration. This may indicate that (1) the condition of the local weather was bad and a bird stayed in the same location for a short time or were forced into powered flight in a head wind, which resulted in a slow ground speed and/or (2) they foraged and replenished energy reserves in a circumscribed location. It is probable that honey-buzzards forage while migrating, because some European honey-buzzards...
migrating with distended crop were reported by Panuccio et al. (2006). Instead of having some long stopover sites, the Oriental honey-buzzard may adopt another strategy of having many very short stay sites, in particular when they are in south-east Asia.

There has been a hypothesis on the large-scale detour and direct crossing of the East China Sea of the autumn migration of this species (Agostini & Mellone, 2007). It explains that the detoured route originates from an innate NE-SW axis that the first colonized individuals retained, and the direct crossing of the East China Sea has an adaptive significance for competition in the wintering quarters with conspecific migrants, as well as conspecific and congeneric residents.

In addition to the hypothesis, here we offer a novel hypothesis on the adaptive significance of the large-scale detoured migration of the Oriental honey-buzzard, based on our analysis of migration state. From the stay state was frequently observed south of 23°26′N but observed less north of that latitude, the migration of Oriental honey-buzzards can be separated into two stages: a temperate stage involving travel to south-east Asia and a tropical stage of repeated local go-and-stay movements. The birds may have evolved to move quickly to arrive in the second stage where more abundant food is available in the tropics. This may suggest that this tropical stage may function as the extended wintering area. This hypothesis can explain why the species’ migration involves such a large-scale detoured route (almost ‘C-shaped’). The segment of the route during the temperate stage (between Japan and northern south-east Asia) is almost linear and the honey-buzzards can minimize their travel distance, although they may encounter some risks by directly crossing the East China Sea. Actually, there was little individual difference in this segment of the migration route. If favourable habitats are distributed fairly evenly across the Malay Archipelago, Borneo and the western Philippines, and travel costs and risks do not differ much, the terminal points of individual migration routes can be widely distributed within the area, and so migration routes to Borneo and the Philippines are C-shaped as a consequence of following the geography of south-east Asia. To test this hypothesis, we need to know the main food of the honey-buzzards in south-east Asia and its spatio-temporal dynamics during the winter season.

Acknowledgements

The authors thank members of the Shinshu Raptor Migration Research Group for their field assistance, Dr Hiroto Shimazaki for his critical advice on analysis, Mr Yasuo Shimada for useful comments on the migration strategy of raptors, Dr Shumpei Kitamura for giving the information on the tropical forests in south-east Asia, Dr Tom Grubb Jr and Jerry W. Hupp for reviewing a draft of this paper and Dr Nicolantonio Agostini and one anonymous reviewer for critical comments on the paper. This research was funded by the Ministry of the Environment in Japan.

References

Green, M., Alerstam, T., Clausen, P., Drent, R. & Ebbinge, B.S. (2002). Dark-bellied Brent Geese Branta bernicla bernicla, as recorded by satellite telemetry, do not minimize flight distance during spring migration. Ibis 144, 106–121.


### Supplementary material

The following material is available for this article online:

**Appendix S1.** The patterns of the daytime travel speeds (km d⁻¹) of 10 adult honey-buzzards in autumn. We coordinated the patterns of travel speeds with geographical locations. Blue bars indicate travel speeds. Each of the adjacent intervals is connected by a grey solid line, but when the distance between two intervals is very long, they are connected by a grey dotted line. The estimation method of the daytime travel speeds is mentioned in the method section.

**Appendix S2.** The pattern of the daytime travel speeds (km d⁻¹) of 10 adult honey-buzzards in spring. We coordinated the patterns of travel speeds with geographical locations. Blue bars indicate travel speeds. Each of the adjacent intervals is connected by a grey solid line, but when the distance between two intervals is very long, they are connected by a grey dotted line. The estimation method of the daytime travel speeds is mentioned in the method section.


Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.