Autumn migration of raptors on Java, Indonesia: composition, direction and behaviour

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The migration of four northern migrant raptors (Oriental Honey-buzzard *Pernis ptilorhyncus*, Chinese Sparrowhawk *Accipiter soloensis*, Japanese Sparrowhawk *A. gularis* and Common Buzzard *Buteo buteo*) was studied in the Dieng mountains, Central Java, Indonesia during September–October 1998. Populations migrating through Central Java originate from northern Asia and most likely have passed over the Thai–Malay peninsula and Sumatra before reaching West and Central Java. An unknown proportion continues on to Bali and/or the Lesser Sunda Islands. In all, 68 groups totalling 885 individuals were counted passing by. Ninety-five percent of individuals identified were accipiters, two-thirds of which could be identified to the species level. Passage was directed from WSW–SW to E–ESE, following the alignment of volcanoes on the island. The number of groups was highest during late morning; single individuals were observed significantly more often during the early morning and large (> 25 individuals) groups during the afternoon. Single individuals and small (five or fewer individuals) groups spent significantly less time in the area than large groups. The forests of the Dieng mountains are also used as an overnight stopover and hunting site. Differences in the proportion of the two species of *Accipiter* identified at Javan and Bali study sites suggests an additional migration route to the one following the Javan mountains. This may follow the eastern edge of the Sunda Shelf. The Dieng mountains qualify as a globally Important Bird Area (IBA) on the grounds of the raptor congregations, as well as because of the presence of globally threatened and restricted range species.

The Asian–Australasian bird migration system is one of the world’s least studied migration systems and, for raptors, only fragmentary information is available on the timing and routes of migration of the northern migrants (Lane & Parish 1991, Coates & Bishop 1997, van Balen 1998, Wells 1999). South of the equator, the Puncak Pass in West Java, Indonesia (A. Long & S. van Balen pers. comm., pers. obs.), islands in the eastern part of the Java Sea (Davison 1997, J.H. Becking in van Balen 1998) and Bali Strait (Ash 1984, 1993) are known passage points, but the huge stretches beyond and between need to be investigated (van Balen 1998).

Hitherto, nine species of raptor have been recorded as migrants on Java during the northern winter. Of these, three (Black Baza *Aricea leuphotes*, Grey-faced Buzzard *Butastur indicus* and Eurasian Hobby *Falco subbuteo*) are rare visitors and normally winter north of Java (van Balen 1984, MacKinnon et al. 1998). One species, Common Buzzard *Buteo buteo* is rarely recorded but has been observed both on Java and Bali, but not yet on Sumatra (MacKinnon et al. 1998; but see Wells 1999 for birds arriving from and heading to Sumatra crossing the Mallaca Straits); the only record from Java seems to be a specimen collected somewhere between 1933–41 (Mees 1971). Both Osprey *Pandion haliaetus* and Peregrine Falcon *Falco peregrinus* are recorded as migrants in the Javan lowlands and along the coast (MacKinnon et al. 1998). The remaining three species (Chinese Sparrowhawk *Accipiter soloensis*, Japanese Sparrowhawk *A. gularis* and Oriental Honey-buzzard *Pernis ptilorhyncus*) are considered regular winter visitors and migrate south to Bali and the Lesser Sunda Islands (Ash 1984, 1993, van Balen 1994, MacKinnon et al. 1998, S. van Balen in litt. 1999). The resident race of the Oriental Honey-buzzard is rarely recorded on Java (van Balen et al. 1999), but as a northern migrant it is common in the Greater Sundas. It has been observed crossing the Bali Strait in the thousands (Ash 1993), although there seem to be comparatively few records for the Lesser Sunda Islands (D. Gibbs in van
Balen 1994, Coates & Bishop 1997, Verhoeve & Holmes 1999, Bishop & Brickle 1999, D. Lesmana pers. comm.). The two accipiters are found in large numbers wintering or in passage. Japanese Sparrowhawk seems to be uncommon, whereas Chinese Sparrowhawk is probably the most common migrant raptor in the region (van Balen 1994).

During a long-term raptor study in the Dieng mountains in the central part of Java, systematic observations were made on migrating raptors. Combined with recent information from birdwatchers and published accounts, the data collected provide some insights into this little-known phenomenon. An overview is presented on raptor passage on the island of Java. The likelihood of including wintering birds in this overview was reduced by, arbitrarily, only including sites where passage was observed for at least two days during which at least 25 birds were recorded.

Specific questions addressed in the present study include the following. What is the representation of species in the migration stream, and what is the approximate total number of individuals passing by? What is the direction of passage movement both over the Dieng mountains and through Java? What is the diurnal timing of passage movement over the day and how does it relate to group size and flight behaviour? Findings from Dieng are compared with other studies that have been conducted on Java and Bali.

MATERIAL AND METHODS

Study area

The study was conducted in the province of Java Tengah, in the Dieng mountains, near the village of Linggo (7°06'S, 109°35'E). The Dieng mountains are still extensively covered with forest ranging from c. 300 m asl in the area north of Linggo to 2565 m asl at Mount Prahu (for a more complete description of the area see Nijman & van Balen 1998).

The study area proper forms part of the northwestern foothills of the Dieng mountains; the altitudinal range lies between 300 and 1310 m asl. Observations were made from a small hill (Mount Blubuk) at an altitude of 600 m asl. Near its summit, on the northwestern slope, a c. 20-m tall watchtower had recently been erected. It provided excellent, unrestricted views from south-southwest to east-northeast. Only in south-southeaster direction was the view somewhat obscured by the summit of Mount Blubuk. On clear days, and especially so during the early hours of the day, Mount Slamet and Mount Ceremai were visible in the west. The latter mountain is situated at a distance of c. 140 km. In the north and northeast the city of Pekalongan and Java's northern coastline were recognizable.

The climate of the study area is perhumid and, with an annual rainfall of c. 6000–7000 mm, is amongst the wettest places on Java. Only during the months July–Sept slightly less rainfall is recorded, but the monthly average remains above 100 mm. Daily maximum temperatures range between 27–31°C. (Climatic data were taken from the nearby weather stations of Semungih, 07°07’S, 109°17’E, and Pagilaran, 07°08’S, 109°50’E, RPPTProT 1990). During the study period it rained almost daily, mostly during the afternoon. It often rained twice a day. Observation conditions were typically poor in the afternoon, as clouds would come in from the valley. Sunrise was at c. 5.20 h local time, and observations were made at all hours of the day, but only during favourable weather conditions, i.e. dry and with a horizontal view of at least 3 km in all directions.

Resident raptors

The resident raptor community near Linggo is diverse. Of the 18 species possible, 11 species near the study site, i.e. Oriental Honey-buzzard Pernis ptilorhyncus (race ptilorhyncus), Crested Serpent Eagle Spilornis cheela, Crested Goshawk Accipiter trivirgatus, Besra A. virgatus, Black Eagle Accipiter nisus, Rufous-bellied Eagle Hieraaetus kienerii, Changeable Hawk Eagle Spizaetus cirrhatus, Javan Hawk Eagle S. bartelsi, Black-thighed Falconet Microhierax fringillarius, Spotted Kestrel Falco naumanni, and Peregrine Falcon F. peregrinus (race ernesti).

The two resident accipiters and the resident race of the Oriental Honey-buzzard may cause confusion with the migrants. During the northern summer, i.e. the non-migration period, however, these three forest species were rarely recorded in the area, suggesting low population numbers at all times. Consistency of flight direction and altitude often provided an additional clue that migratory birds were involved rather than residents.

Data acquisition and analysis

Observations on migrating raptors were made during 22 September to 12 October and 17–31 October 1998. On 22 of the 36 days, observations were made from the watchtower. Others were spent mostly inside the forest where sighting raptors was more difficult. For observation purposes 12 x 50 binoculars were used, and a compass for following flight directions. The
methodology of spotting raptors generally followed Bildstein and Zalles (1995), e.g. the sky from where migrants were expected was methodically scanned using clouds and distance landmarks as a frame of reference for distance focusing. Special attention was paid to aggregations of resident raptors and storks as these tend to indicate good flight conditions that may be conducive to migration. In order to reduce bias due to observer fatigue, observation bouts lasted a maximum of 4 h. Because of low cloud, it was not always possible to identify the species of raptor passing by. Occasionally whole flocks of raptors ‘disappeared’ into the clouds. Of the migrants, the two accipiters were sometimes difficult to distinguish, and they were occasionally in mixed flocks. In addition to diagnostic colour patterns, differences in appearance were used for identification of the two species: Japanese Sparrowhawk seemed to have proportionally shorter and broader wings.

Every individual or group that came in sight was followed as long as viewing allowed. Continuous recording started immediately upon sighting and behaviour was recorded in 30 s intervals. The following activity categories are considered in this paper: (i) sustained flapping flight, characterized by a deliberate flapping movement of the wings; (ii) gliding, characterized by a straight line movement without noticeably using the wings; (iii) soaring, characterized by the birds rising on thermal updrafts; (iv) miscellaneous behaviour, such as hunting in or above the forest.

A group is defined as a spatially and temporally stable cluster of birds, members of a group spending at least 30 s in close proximity. By definition, groups travel in a single general direction. If not, a group splits into two or more smaller groups. Similarly, two or more groups can fuse into a larger group. For analysis, four different group sizes were distinguished: single birds, small (five or fewer individuals), medium (six to 25) and large (> 25). In analysing the behaviour of migratory birds of prey, the group was considered the appropriate unit of measurement to avoid pseudo-replication (Martin & Bateson 1993).

For analysis, the day was divided into four equal periods: early (06:01–09:00 h) and late (09:01–12:00 h) morning, and early (12:01–15:00 h) and late (15:01–18:00 h) afternoon.

The average number of migrating raptors per day at Linggo was estimated by multiplying the average number of groups observed per time interval with the average group size for that time interval. In order to obtain an indication of the total number of migrating raptors passing during the study period this was multiplied by the observed migration period in days (last date minus first date).

As little is known about the nature of the (statistical) populations from which the samples are drawn, and in order to increase the generality of the conclusions, non-parametric statistical tests were used (Siegel 1956). Yates’ correction for continuity was applied in the chi-squared test applications when appropriate. Significance was accepted when $P < 0.05$ in a two-tailed test.

**RESULTS**

**Species composition**

During the 22 observation days, 86 hours were spent on the look-out for raptors mainly from the watchtower. Migrant raptors were observed on 13 days. Most observations refer to passing birds. Chinese Sparrowhawks were recorded twice hunting in the forest; once a single bird and once two birds in close proximity. On the morning of 28 October at 10.53 h, a large group (c. 110 birds) of mainly Chinese Sparrowhawk and some Japanese Sparrowhawk was observed ascending from a valley.

The first migrant was observed on 29 September, whereas on the last observation day (31 October) migrants were still passing. The first Oriental Honey-buzzard was observed on 7 October and the last on 27 October. For Chinese Sparrowhawk and Japanese Sparrowhawk, these dates were 29 September to 31 October, and 7–31 October, respectively. In all, 68 groups were counted passing by, totalling 885 individuals (median group size 3, range 1–130). Extrapolating from observation bouts to migration days, on average 105 raptors per day must have passed the study site. Over the 33 days of migration this extrapolates to c. 3500 individuals. The migrants comprised four species. Ninety-five percent of the individuals belonged to one of the two accipiters, over two-thirds of which could be identified at the species level (Table 1). The rest were Oriental Honey-buzzards, with a single record of Common Buzzard.

Since the vast majority of records are accounted for by the two accipiters, only part of which could be identified to the species level and as mixed flocks occurred regularly (which also included Pernis), in the analysis of flight direction, timing and behaviour no further distinction is made between species. Furthermore, group members were mostly engaged in the same activity, supporting the assumption that individuals in a group do not behave independently.
Table 1. Numbers and proportion of migrant raptor species observed during the autumn on Java and Bali, Indonesia. Localities are listed from west to east.

<table>
<thead>
<tr>
<th>Site</th>
<th>Period (no. of observation days)</th>
<th>Chinese Sparrowhawk Accipiter soloensis</th>
<th>Japanese Sparrowhawk Accipiter gularis</th>
<th>Unidentified Sparrowhawksb Accipiter spp.</th>
<th>Oriental Honey-buzzard Pernis ptilorhyncus</th>
<th>Total no. of birds observed</th>
<th>Source[^2]</th>
</tr>
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[^a]: Numbers refer to those in Fig. 1.  
[^b]: Note that Ash (1993) included an unknown proportion of unidentified accipiters as either Chinese or Japanese Sparrowhawks. 

**Direction of flight on Java**

From 42 groups (totalling 540 individuals) it was possible to assess the direction of arrival: 40% of the groups (70% of the individuals) came from a WSW-SW direction (200-235°). From 38 groups (totalling 756 individuals) the direction of departure was assessed: 71% of the groups (72% of the individuals) flew off in an E-ESE direction (83-113°). Unlike the situation at the Puncak Pass or at the Bali Strait, the passing raptors near Linggo are not compressed into a migratory bottleneck. Instead, given the topography of the area, the birds probably passed along a broad front of several kilometres (c. 15 to > 20 km). The main direction of arrival suggests that the birds came from Mount Slamet and surroundings, while departure was in the direction of Mount Prahu, following the dominant direction of the Dieng mountain chain.

An unknown proportion of the populations of raptors migrating over Java must have overflown parts of Sumatra before entering Java. Although little is known about migration routes on Sumatra, one route follows the eastern coast, as passage has been recorded over Way Kambas (no. 1 in Fig. 1: 7-9 November 1999, including 188 accipiters and 20 Oriental Honey-buzzards, pers. obs.) before reaching the Sunda Strait (no. 2). Here raptor migration was recorded both on the Sumatran side (Bakauheni, 38 accipiters and 25 Oriental Honey-buzzards) and the Javan side (Merak, 17 accipiters and 13 Oriental Honey-buzzards) (pers. obs. 6 and 9 November 1999).

Other localities on Java where autumn migration of raptors has been observed are (numbers refer to those in Figure 1): (3) Pulau Dua, 4-5 October 1984, including 63 accipiters and 18 Oriental Honey-buzzards (Allport & Wilson 1986); (4) Darmaga, 11, 19 and 29 October 1997, including 26 accipiters (K.P.B. Prenjak in litt. per R. Saryanthi); (5) Puncak Pass, regularly since October 1996, comprising Oriental Honey-buzzards, Chinese and Japanese Sparrowhawks (Rudyanto, A. Long & K. Koyama pers. comm.); (6) Jatingangor, 1-4 October 1996, 47 unidentified raptors and one Chinese Sparrowhawk (F. Hadi, D.S. Priyadi & H.A. Singer in litt. per R. Saryanthi); (7) Mount Slamet, 20-21 October 1999, including 45 Chinese Sparrowhawks (I. Setiawan, pers. comm.); (9) Mount Ungaran, 9-10 October 1998, total of 86 Chinese Sparrowhawks (F. Arga Narata & Sugiharto pers. comm.) (10) Mount Semeru, end of October 1998, 'flocks of unidentified raptors' (R. Nursaid pers. comm.); (11) foothills of Mount Ijen (Banyuwangi), late 1941, comprising mainly accipiters (observed by the late J.G. Kooiman, J.H. Becking in litt. 1999).

On Java, apart from the first two and possibly also the last, sites mentioned, all localities are essentially situated along the central Javan mountain chain or on the volcanoes themselves. Despite research at appropriate elevations, mass raptor migration has not yet been observed at any lowland site on Java or Bali, apart from those sites where birds make a landfall. Hence, it seems that the volcanoes on Java act as 'leading lines' (sensu Bildstein & Zalles 1995) for raptor migration.
Timing and behaviour

The earliest migrant of the day (a single Chinese Sparrowhawk) was observed at 07:15 h, whereas the latest (a group of 20 Chinese Sparrowhawks) were observed at 16:20 h. Although in the early morning the passing migrants were mostly engaged in flapping flight whereas soaring seemed to peak during the late morning, there was no significant relation between mode of flight and time of day ($\chi^2 = 1.56$, ns; early and late afternoon were pooled so as to avoid too many expected values < 5). The number of groups observed during different intervals of the day differed significantly ($\chi^2 = 15.1$, $P < 0.01$), but only during the late morning (09:01–12:00 h) were more groups observed than expected if time of passage had been homogeneously distributed through the day (1.5 v. 0.4 groups per hour, $\chi^2_i = 13.0$, $P < 0.001$).

Group-size incidence varied between periods of the day ($\chi^2 = 15.3$, $P < 0.02$; early and late afternoon pooled to avoid too many expected values < 5). Thus, during the early morning significantly more single individuals were observed than expected by chance whereas during the afternoon more large groups were observed than expected by chance ($\chi^2_i = 4.17$, $P < 0.05$ and $\chi^2_i = 4.30$, $P < 0.05$, respectively).

The total observation time was not related to flight behaviour (Kruskal–Wallis, $H_z = 3.4$, ns) but differed between groups of different sizes ($\chi^2 = 22.34$, $P < 0.001$). The average time spent in the area by groups decreased significantly with decreasing group size; single individuals and small groups were observed for a median of 1.30 min, medium groups for 2.00 min and large groups remained in sight for 4.15 min (Kruskal–Wallis $H_z = 24.3$, $P < 0.001$). This allows for further significance testing of the data set. Only single individuals and small groups spent significantly less time in the area compared with large groups (Mann–Whitney $U$, both $P < 0.05$). Although the time spent in flapping flight, gliding or soaring differed significantly between the four group sizes ($\chi^2 = 13.1$, $P < 0.05$) – for example, single individuals tended to spend more time in flapping flight – and large groups to spend less time gliding and more time soaring, none of these tendencies differed significantly from a random pattern.

DISCUSSION

Migration routes of Javan migrants

The species of migrating raptors observed on Java (and Bali) consist of birds originating from eastern Asia, probably including southern China and Japan, where they breed in the forest and steppes (del Hoyo et al. 1994, van Balen 1994, Wells 1999). Most are likely to have passed over the western half of Java, possibly much of Sumatra and the Thai–Malay peninsula, before reaching the Dieng mountains. An unknown proportion migrates further to Bali and/or the Lesser
Sunda Islands, but their final destination remains largely unknown. None of the Southeast Asian migratory raptors reaches mainland Australia or mainland New Guinea (Lane & Parish 1991, del Hoyo et al. 1994, Beehler et al. 1986).

To date, systematic counts of migrating raptors on Java and Bali have been made only at the Puncak Pass (S. van Balen & A. Long unpubl. data), Linggo (this study), Gilimanuk-Banyuwedang (Ash 1984) and Teluk Terima (Ash 1993). At all four sites, the raptors comprised principally the same three species. Most abundant were the two species of Accipiter, making up between 80% and 95% of the raptors observed. Interestingly, at the two Javan sites, the most abundant raptor was Chinese Sparrowhawk with only a small number of Japanese Sparrowhawks, whereas of the birds arriving at Bali, the majority were Japanese Sparrowhawks (Table 1).

Ratios of the two species of Accipiter identified at the West and Central Java study sites differ from those of Bali – on Java the ratio of Chinese Sparrowhawk to Japanese Sparrowhawk was 41:1 and 35:1 for the Puncak Pass and Linggo, respectively, whereas on Bali it was 1:2 at Gilimanuk-Banyuwedang and 1:8 at Teluk Terima. Comparing the numbers of the two accipiters between the two Javan sites, there are no significant differences ($\chi^2_1 = 0.23$, ns), whereas within Bali there are ($\chi^2_1 = 190.1, P < 0.0001$), just as there are between the Javan sites (pooled) and two Balinese sites ($\chi^2_2 = 6407.5, P < 0.0001$). The differences between the Bali study sites may be related to differences in timing and duration of observation (Ash 1993). Assuming correct identification and no bias in the chances of not identifying one of the two species, and excluding the existence of large intra-annual variation, the most plausible explanation of the differences between the sites is the existence of an additional migration route, besides the one following the Javan mountains. An alternative explanation, that the Chinese Sparrowhawk drops out of the migration stream, can be excluded by comparing the differences of absolute numbers of Japanese Sparrowhawk between Java (52 birds in 30 days) and Bali (8179 birds in 39 days) (Table 1).

Possible candidates for this additional migration route follow either Java’s flat northern coastline, Java’s rugged south coast, or the eastern part of the Java Sea. Since no raptor passage has been observed to date along the first two routes, the most plausible route for such an additional migration follows the islands along the eastern edge of the Sunda Shelf (Fig. 1). Thus, Simpson (1983) observed > 40 Japanese Sparrowhawks and a single Chinese Sparrowhawk migrating over the South China Sea off Sabah, North Borneo (September–October 1981). South of Borneo, Davison (1997) observed a southwestern raptor migration of Japanese Sparrowhawks at sea south of Laut Island (14 October 1996), over Marabatuan Island and between Matasirih and Kalambu Island (15–16 October 1996). From 31 October to 15 November 1997, raptor migration (including c. 60 accipiters and > 180 Oriental Honey-buzzards) in an east to west direction was observed on Masa Kambang Island (F. Arga Narata, pers. comm.). Birds following this route probably enter Java on the northern coast of the East Java province, and might turn east upon reaching Java. Additionally, migrating raptors have been observed reaching western Bali from the north (I.Z. Mutaiqin in litt. 1996, per R. Saryanthi) indicating that some of the migrants arriving in Bali may be on a more or less direct flight from the north, rather than having overflown much of Java.

### Numbers of passing migrants

During this study, birds were often within clouds and appeared only when the cloud lifted. Although at Linggo observations were made when there was a horizontal view of at least 3 km in all directions, afternoon low-hanging cloud, in particular, restricted the vertical view. At these times the numbers of birds might have been underestimated. Furthermore, many raptors arriving at Bali after crossing the Bali Strait were flying at great heights (often above 1800 m, Ash 1993). High-flying birds may have been missed. For these reasons, the estimate of c. 3500 migrating raptors must be conservative. Since migrants were observed even on the last observation day (31 October), migration presumably continued into the second half of November or even later (see also data from the Thai–Malay peninsula, where raptor migration continues into December; Wells 1990, 1999). Moreover, only part of the possible wide migration front may have been in view. The total number of raptors migrating through the Dieng mountains may have exceeded 10000. The first migrants arriving in the morning were usually flying low, often in active flight and had most likely been roosting in the vicinity. The group of over a hundred accipiters observed ascending from a valley in the morning strongly suggests that the forests near Linggo are used as a roosting site. Hitherto, the only large roosting site for raptors on Java has been recorded in the valleys near the Puncak Pass, where hundreds of raptors congregate for the night (Rudiyanto pers.
Conservation of migratory raptors

Java is largely deforested and most of the remaining forest fragments cover (parts of) the numerous volcanoes on the island. Less than 10% of the island’s land coverage remains forested; the remainder is essentially a mosaic of rice fields, cities and villages (Whitten et al. 1996). Favourable habitat, where a migrant can safely and rapidly accumulate energy stores, is probably limited, or is effectively limited because a migrant may not have the opportunity to select the best stopover sites (Moore & Spina 1998). Maintenance of forest cover at stopover sites is essential as environmental changes at these sites have the potential for significant impact on entire flyway populations. Based on the criteria set by BirdLife International (Grimmett & Jones 1989; Rudiyanto pers. comm.), the Dieng mountains would qualify as a globally important bird area (IBA), under criterion A4 (congregations), in addition to criteria A1 (globally threatened species: 2 spp.) and A2 (restricted range species: 23 spp) which have already classified the Dieng mountains as an IBA. Considering the unprotected status of the forests in the Dieng mountains, and recognizing the importance of the area for global bird conservation, proposals have been put forward to include the Dieng mountains in Java’s conservation area network (Nijman & Sözer 1996).

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REFERENCES


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