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Habitat segregation in two congeneric hawk-eagles (*Spizaetus bartelsi* and *S. cirrhatus*) in Java, Indonesia

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Abstract: On the island of Java, Indonesia, two congeneric hawk-eagles occur, i.e. the endemic Javan hawk-eagle *Spizaetus bartelsi* and the wide-ranging changeable hawk-eagle *S. cirrhatus*. Comparisons with similar species-pairs in South-East Asia suggest that these species may be competitors both in habitat and diet. The limited area and less-diverse resources of islands should make competition between similar species more acute and should lead to marked niche segregation, with a larger niche breath for the endemic species. *Spizaetus bartelsi* was recorded significantly more frequently in forest habitats from sea level to 2500 m asl and *S. cirrhatus* more in open habitats up to 1600 m asl. Contrary to the prediction, the endemic hawk-eagle occurred in a smaller range of habitats (four out of seven) compared with *S. cirrhatus* that was found in all seven habitat types. Although significant, habitat segregation was not as well marked as in some similar co-occurring *Spizaetus* species. The relative overlap between the two species may in part result from human influences with the dense continuous rain forest being replaced by more open forest types.

Key Words: changeable hawk-eagle, Falconiformes, habitat preferences, Javan hawk-eagle, raptors

INTRODUCTION

Understanding the patterns and mechanisms of the co-existence of (morphologically similar) species within local assemblages is one of the major issues addressed in contemporary community ecology (Pianka 1981, Wiens 1989). On the island of Java, Indonesia, two congeneric hawk-eagles occur, i.e. the endemic Javan hawk-eagle *Spizaetus bartelsi*, Stresemann, 1924 and the more widely occurring changeable hawk-eagle *S. cirrhatus* (Gmelin, 1788). In the Sundaic region and in the Philippines, where it occurs in sympatry with one or two other *Spizaetus* hawk-eagles, *S. cirrhatus* is restricted to open woodlands and degraded forest, with its congener occurring more in closed forest types (Philippines, Philippine hawk-eagle *S. philippensis*, Gould, 1863: Gamauf *et al.* 1998, Sumatra, Blyth's hawk-eagle *S. alboniger* (Blyth, 1845): Thiollay 1996, Borneo, *S. alboniger* and Wallace's hawk-eagle *S. nanus* Wallace, 1868: V. Nijman unpubl. data). In those parts of its range where it does not live in sympatry with another *Spizaetus* hawk-eagle (India, Vietnam, the Andamans) *S. cirrhatus* occurs in primary forest as well as in more open secondary stands (Thiollay 1998), and on the Andamans it actually prefers primary forests (Thiollay 1997). Similar observations have been made on the Floris hawk-eagle *S. (c.) floresi* Hartert, 1898 of the Lesser Sunda Islands (Z. Rahman *pers. comm.*, V. Nijman unpubl. data). On the other hand, on Sulawesi, where *S. cirrhatus* does not occur, the Sulawesi hawk-eagle *S. lanceolatus* Temminck & Schlegel, 1844, a species closely related to *S. bartelsi*, *S. alboniger*, and *S. philippensis*, occurs both in forested and more open habitat types (Meyburg & van Balen 1994, V. Nijman *pers. obs.*, S. van Balen *pers. comm.*). These observations suggest that competition plays a role and, hence, the co-existence of the two hawk-eagles on the island of Java poses interesting questions in the light of the competitive exclusion principle (Krebs 1994).

Thiollay & Meyburg (1988) found evidence of the so-called insular syndrome (Blondel 2000) in the raptors of Java. A primary attribute of this syndrome is the higher density often reached by island populations compared with those of continental populations in similar-sized areas, possibly due to fewer competitive interactions and reduced intraspecific aggression or territorial defence (Stamps & Buencher 1985). A second component of the

insular syndrome is niche expansion, mostly documented as an increase in habitat niche breadth (Blondel 1985, Wiens 1989). At the same time, the limited area and the less-diverse resources available on islands compared with similar-sized continental areas should make competition between similar species more acute. This should lead to marked habitat shifts and niche segregation (Williamson 1981). On New Caledonia, Thiollay (1993) found the insular syndrome to be less marked for a wide-ranging raptor (*Accipiter fasciatus*) compared with an island endemic (*A. haplochrous*). The endemic had a broader habitat range, a broader range of hunting behaviour and prey items, and occurred at higher densities than its wide-ranging congener.

Like most endemic birds on Java, *S. bartelsi* is an evergreen-forest specialist as the island used to be entirely forested (Whitten *et al*. 1996). Always described as being rare, until recently the species was one of the world's least-known raptors, with basic data on feeding behaviour, geographical distribution, habitat preference, breeding, etc. completely lacking (Ferguson-Lees & Christie 2001). Currently, after being declared as Indonesia's national rare animal (Widyastuti 1993), the eagle is among the most studied birds in Indonesia (van Balen *et al*. 1999*a*, 2000, 2001).

Spizaetus cirrhatus has a much wider distributional range than *S. bartelsi*, occurring throughout East Asia. It is a specialist of forest edge and semi-open woodland (Ferguson-Lees & Christie 2001). Initially its habitat on Java was doubtless greatly expanded by deforestation that commenced around the tenth century AD (Whitten *et al*. 1996). Formerly considered a common species on Java (Bartels 1924, A. Hoogerwerf unpubl. ms), population numbers of *S. cirrhatus* appear to have declined considerably over recent decades. Currently it is less frequently encountered on Java than on other Sundaic islands (van Balen 1994, S. van Balen & V. Nijman, unpubl. data). No detailed studies on *S. cirrhatus* have been conducted on Java.

Resource partitioning in birds is most frequently studied along two of the niche-axes, i.e. habitat and diet and/or their derivatives (Thiollay 1993, Wiens 1989). The feeding behaviour of *S. bartelsi* has been studied in some detail (D. M. Prawiradilaga, unpubl. data), but most data originates from opportunistic observations (Nijman *et al*. 2000). It is believed to prey on a wide variety of animals, including reptiles, birds and small mammals. The diet of *S. cirrhatus* includes amphibians, reptiles, birds and mammals (Ferguson-Lees & Christie 2001), on Java it possibly has a preference for birds (Bartels 1924, Hoogerwerf 1949). Despite an expected overlap in diet, and hence the potential for competition, given the difficulties in systematically studying the feeding ecology of low-density and generally uncommon raptors, the present study focused entirely on habitat segregation as a resource-partitioning mechanism.

Hence, I report on relative habitat use of the two congeneric hawk-eagles on Java. If the insular syndrome is valid for these two raptors a marked habitat segregation between the two species is expected, and furthermore, if the insular syndrome is less pronounced for the wide-ranging *S. cirrhatus* as compared with the endemic *S. bartelsi*, as postulated by Thiollay (1993) for New Caledonian raptors, one would expect niche breadth to be greater in the latter species.

STUDY AREA

Java (126 500 km^2), Indonesia's political and industrial centre, is one of the most densely populated areas in the world (Whitten *et al*. 1996). The island is largely deforested with most of the remaining 10% forest covering the numerous volcanoes on the island. It has been replaced by a mosaic of cities and villages, agricultural land, cash-crop plantations (e.g. coffee *Coffea* sp.), and forest plantations (teak *Tectona grandis*, Sumatran pine *Pinus merkusii*, rubber *Hevea brasiliensis*).

The climate of Java differs greatly over the length of the island. The eastern part and the north coast have a pronounced dry season, the western half does not. Rain forest occurs in areas where the length of the dry season is short, on Java coinciding with areas that have at least 30 rainy days during the four consecutive driest months of the year (van Steenis & Schippers-Lammertse 1965). In the drier areas wet forest is replaced by moist or deciduous forest.

MATERIAL AND METHODS

Data acquisition

Tropical forest raptors are notoriously difficult to observe. Thiollay (1989) estimated to observe, on average, only one raptor per day while walking inside primary forest areas. In Japan the mountain hawk-eagle *S. nipalensis* spends 95% of daytime perched inside the forest and on 20% of days it does not fly at all (T. Yamasaki, *pers. comm*.). Given this, I chose to assess the presence of hawk-eagles by scanning large areas from vantage-points and searched the sky and canopy. Inside forest areas their presence was established mostly aurally by their characteristic vocalizations (Nijman & Sözer 1997). For observations, sites were selected on high vantage points and while in the forest use was made of either small forest trails or transects. Eagles are most active between 08h00–13h00, and most observations were made during the late morning and early afternoon.

Hawk-eagles were studied during all months of the year from 1994–2000, with a total survey effort of *c.* 300 d. The study covered 25 isolated forest areas in Java, from its westernmost tip at Ujung Kulon to its easternmost at Baluran, in addition to numerous smaller study areas (van Balen *et al.* 1999*a*). Over 80% of the survey effort was outside the established protected area network.

For each bird the habitat in which it was first encountered (either perched or flying) was recorded. In general the habitats recognized covered substantial areas and only rarely was it not possible to assign a recording to one habitat type. In that case each of the two habitats received half a score. Each recording was assigned an altitude, being the altitude of the habitat in or above which the bird was recorded and not the altitude of the bird itself (in case of aerial records). Hawk-eagles are territorial and frequently perform aerial displays (Ferguson-Lees & Christie 2001, Nijman *et al.* 2000) and often select specific sites to perform this type of behaviour. In order to reduce bias due to pseudo-replication, individual birds encountered on subsequent days at (nearly) the same site were included only once in the analysis.

Habitat types

Seven habitat types were recognized. From the more open to the more dense they are:

(1) Cultivated Land, including grassland, secondary growth, agricultural land (including tea plantations and wet rice-fields) and village areas.
(2) Woodland, including open woodland, large clearings and small forest fragments, and young tree plantations (Sumatran pine, rubber).
(3) Coastal Forest, including 5–10 m low mangrove forest, mainly consisting of *Rhizophora* spp., *Bruguiera* spp. and *Avicennia* spp., and fringes of low mixed beach forest, characterized by *Barringtonia asiatica* trees. Mangroves on Java occur in small pockets mainly along the north coast. Small stretches of beach forest are found mainly in reserves like Ujung Kulon and Baluran. In total Coastal Forest covers an area of less than 200 km^2.
(4) Teak Forest, consisting of monocultures of mature teak trees. Teak plantations on Java are managed by Perum Perhutani (the state forestry department) and contain little undergrowth. Locally it alternates with small patches of alang-alang *Imperata cylindrica* grassland. Strips of gallery forest are often left along water courses which might provide nesting sites for hawk-eagles. Occurs mainly in the eastern and northern part of Java covering an area of *c.* 6000 km^2.
(5) Deciduous Forest, including sub-mature and moderately disturbed deciduous forest with a low canopy. Like Teak Forest, Deciduous Forest occurs mainly in the eastern and northern part of Java, and covers an area of less than 1000 km^2.
(6) Secondary Forest, including highly degraded natural forest with dense undergrowth and dominated by isolated trees, secondary forest, either heavily logged or naturally disturbed (slopes, volcanic activities), (sub-) mature tree plantations (Sumatran pine, rubber, damar or kauri *Agathis dammara*, and mahogany *Swietenia* spp.).
(7) Evergreen Forest, including sub-mature, moderately disturbed evergreen natural forest with a continuous canopy, and large tracts of high undisturbed forest. Occurs mainly in the western and central part of Java, and on the wetter slopes of high mountains in the east, covering an area of *c.* 10 000 km^2.

When considering altitude a distinction was made between altitude per se (i.e. the elevation asl) and the local relief of the terrain. In mountainous areas in Java large flat plateaux may be present, whereas in lowland areas certain parts can be very steep. Lowland here is defined as altitudes < 1200 m asl and montane as > 1200 m asl. On Java, generally, the 1200 m altitude line is the approximate upper limit where the lowland forest formation gives rise to the montane forest formation (Whitten *et al.* 1996) and where the lowland avifauna is almost completely replaced by a montane avifauna (S. van Balen & V. Nijman, unpubl. data).

Statistical analysis

Different amounts of time were spent in the different habitats with a bias towards the wetter and less disturbed types and detectability of eagles, both visually and aurally, seemed to differ significantly between habitats and between observation sites. However, the likelihood of detecting either species within habitats and within sites probably does not differ. On Java both species are of similar size, differing less than 7% in wing-length (Wijsman 1963), both emit similar pitched calls with a frequency of around 3.9–4.3 kHz (Nijman & Sözer 1997) and the aerial displays of each peak between 08h00–13h00 (Nijman *et al.* 2000).

Because most of the data collected were not normally distributed, non-parametric tests were used (Siegel 1956). For testing whether observed frequencies of occurrence are homogeneously distributed over all classes, and whether significant differences exist between the different classes, χ^2-tests were used. When sample sizes were too small a G-test of goodness of fit for single classification frequency distributions was used. To obtain a better approximation to χ^2 William's correction to G was applied (G_{adj}: Sokal & Rohlf 1995). G_{adj} values were compared

with critical values of the χ^2-distribution. Significance was assumed when $P < 0.05$ in a two-tailed test, and trends are mentioned when $0.05 < P < 0.10$.

RESULTS

Numbers

At least 45 *S. bartelsi* were recorded in 12 areas, and at least 59 *S. cirrhatus* were recorded in 20 areas. Both species range over vast areas (with homeranges in the order of 5–45 km^2, van Balen *et al.* 2001), and of 24 *S. bartelsi* and 18 *S. cirrhatus* it was not possible to ascertain whether or not they represented birds recorded earlier at a different, but still nearby, locality. On three occasions both species were recorded side by side, but mostly the former was encountered in the interior of forest areas and the latter along the edge or outside forest areas. *Spizaetus bartelsi* was most frequently recorded as singles or in pairs, sometimes accompanied by a single juvenile, i.e. rarely more than three birds at a time. *Spizaetus cirrhatus* in contrast, especially in eastern Java, were occasionally observed in groups of several, up to five, birds. Given the length of the study and the amount of ground covered, the total number of birds recorded is low. This is in part due to the conservative methodology employed, i.e. birds encountered on different days at similar sites were included only once in the analysis, but in part this is also due to the genuine rarity of both species on Java (cf. Thiollay & Meyburg 1988).

Although the frequency of encounters (Table 1) is not a measure of abundance and only allows a relative comparison of habitat use between species, the total number of records correctly indicates that both species are approximately equally rare on the island. Compared with similar studies (Gamauf *et al.* 1998, Thiollay 1998, V. Nijman, unpubl. data) this points to the relative rarity of *S. cirrhatus* on Java.

Table 1. Records of two congeneric hawk-eagles in different habitat types on Java, Indonesia (1994–2000).

Habitat	Javan hawk-eagle *Spizaetus bartelsi* (% of total observed)	Changeable hawk-eagle *Spizaetus cirrhatus* (% of total observed)
Cultivated land	9 (13)	23 (30)*
Woodland	3 (4)	13 (17) *
Coastal forest	0 (0)	1 (1)
Teak forest	0 (0)	3 (4)
Deciduous forest	0 (0)	8 (10)**
Secondary forest	15 (22)	19 (25)
Evergreen forest	42 (61)	10 (13)*
Total	69	77

* $P < 0.05$, ** $P < 0.01$ (binomial test).

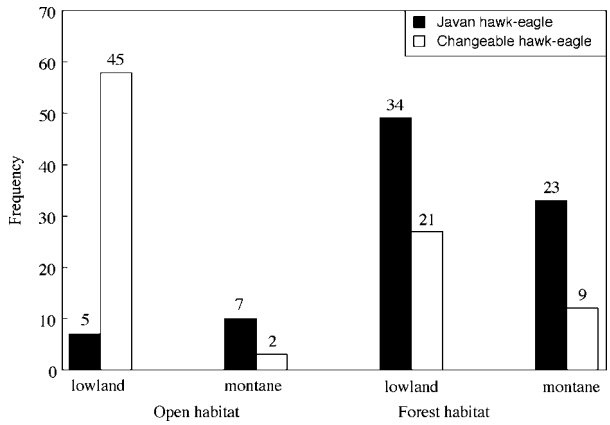

Figure 1. Habitat segregation of two congeneric hawk-eagles *Spizaetus bartelsi* (Javan hawk-eagle) and *S. cirrhatus* (changeable hawk-eagle) on Java, Indonesia. Forest habitats are: Secondary Forest and Evergreen Forest; open habitats are: Cultivated Land, Woodland, Coastal Forest, Teak Forest and Deciduous Forest (see text for details). Lowland habitats are below 1200 m asl, and montane habitats are above 1200 m asl. Numbers above the bars are sample sizes.

Habitat use

Spizaetus cirrhatus was recorded in all seven habitat types recognized (Table 1), in lowland as well as montane areas (excluding Beach Forest, Teak Forest and Deciduous Forest which only covered lowland) (Figure 1). *Spizaetus bartelsi* was recorded in four of the seven habitat types recognized, both in lowland and montane parts. The frequency of occurrence in the different habitat types differed significantly between the two species ($G_{adj.} = 49.9, df = 6, P < 0.001$), allowing for significance testing of part of the data set. Compared with *S. bartelsi*, *S. cirrhatus* occurred more often in Cultivated Land ($\chi^2 = 6.0, df = 1, P < 0.02$), Woodland ($\chi^2 = 5.9, df = 1, P < 0.02$) and Deciduous Forest ($G_{adj} = 5.3$, $df = 1$, $P < 0.05$) than in the other habitat types combined. *Spizaetus bartelsi*, in contrast, was significantly more often observed in Evergreen Forest than in the other habitat types combined ($\chi^2 = 36.3$, $df = 1$, $P < 0.001$). Overall, *S. bartelsi* was more frequently recorded in forest habitats (i.e. Secondary Forest and Evergreen Forest) and *S. cirrhatus* more in open habitats (Cultivated Land, Woodland, Beach Forest, Teak Forest and Deciduous Forest) ($\chi^2 = 30.4$, $df = 1$, $P < 0.001$: Figure 1). Hence both species are clearly segregated by habitat, and they exhibited complementary distributions along the habitat gradient.

Spizaetus cirrhatus was not recorded proportionately more often in the dry eastern part of Java (east of 110° longitude) compared with the wet western half ($\chi^2 = 2.0$, $df = 1, P > 0.10$). However, the number of birds observed in areas with more than 30 rainy days during the four driest consecutive months of the year compared with

the number of birds observed in areas with less rainy days, differed between the species. *Spizaetus bartelsi* was significantly more likely to be found in areas with a less-pronounced dry season compared with *S. cirrhatus* ($\chi^2 = 11.9$, df = 1, $P < 0.001$).

Altitudinal distribution

Spizaetus bartelsi had the larger altitudinal range of the two hawk-eagles. It was found from sea-level to 2500 m asl, whereas *S. cirrhatus* was found from sea-level up to 1600 m asl. This corresponds well with published data (500–3000 m asl for *S. bartelsi* and 0–1500 m asl for *S. cirrhatus*: Ferguson-Lees & Christie 2001). The difference between the species in the number of birds observed in lowland (< 1200 m asl) compared with montane (>1200 m asl) areas is significant ($\chi^2 = 8.4$, df = 1, $P < 0.01$) (Figure 1). Hence, *S. cirrhatus* is more restricted to the lowlands than *S. bartelsi*. *Spizaetus bartelsi* was recorded significantly less often on flat terrain (3 out of 45 records) compared with *S. cirrhatus* (17 out of 60 records) ($\chi^2 = 7.8$, df = 1, $P < 0.001$).

DISCUSSION

General findings

One prominent outcome of this study is the rarity of both hawk-eagles and the low numbers observed. In part this might be related to the design of the study with an emphasis on areas outside the protected area network. Indeed, Thiollay & Meyburg (1988) stated that 'among over 50 countries we have counted raptors, we have never seen one where raptors were so rare outside reserves [as on Java]'. Possible causes for the rarity of birds of prey on Java are severe deforestation and intensive land-use, use of pesticides, 'sports'-hunting, and trapping for the cage-bird trade (Holmes 1996, van Balen & Nijman 2003, van Balen *et al.* 1993). For low-density species such as *S. bartelsi* that breeds once every 2 y when one young is produced (Nijman *et al.* 2000), the removal of a small number of chicks or the added death of a small number of adults due to hunting or capturing can have a great influence on population parameters (Wasis *et al.* 1996). All raptors are protected by Indonesian law and, despite law enforcement being weak, it would be difficult to accurately assess the precise effect that humans have on densities of local populations of forest eagles.

Habitat segregation

Spizaetus bartelsi was recorded in four of the seven habitat types recognized, covering a large altitudinal range, but were not recorded in Teak Forest and rarely in forest plantations or cultivated land. However, van Balen *et al.* (2000), argued that aggregations of smaller forest areas (including Evergreen Forest or Secondary Forest) may not appear as archipelagos when the intervening matrix has a low degree of habitat difference (i.e. it is still partially forested and only extensively used). In effect it may be considered as composites cemented by mature plantations and agricultural land. On Java some 17% of the agricultural land consists of home gardens and their forest-like structure more or less mimics natural forest (Whitten *et al.* 1996). The presence of *S. bartelsi* in long-isolated forest patches (van Balen *et al.* 2000), which on their own may not be large enough to support a viable eagle population, suggests a role of the surrounding (non-forest) habitat as it increases the effective size of the small forest areas. Likewise, plantations may increase connectivity (the degree to which the landscape facilitates or impedes movement among resource patches: Taylor 1993) and explain the persistence of *S. bartelsi* in isolated forests in the dry eastern part of Java.

Spizaetus cirrhatus was recorded in all seven habitat types, including dry habitat types such as Teak Forest and Deciduous Forest. *Spizaetus cirrhatus* seem to be genuinely more common in the eastern part of Java, although in the present study no difference was found in the ratio of the two species in the western half of the island compared to the eastern half.

A number of researchers have addressed habitat segregation between *S. cirrhatus* and a congener. In the south-western Ghats, India, and western Sumatra, Thiollay (1996) found habitat segregation between *S. cirrhatus* and *S. nipalenis* (Ghats) and *S. alboniger* (Sumatra) to be almost complete. Only in heavily logged or disturbed and agroforest did the two species co-exist. Gamauf *et al.* (1998) found that *S. cirrhatus* and *S. philippensis* co-exist in well-wooded habitats, but the former occurred more typically in a mosaic of degraded and fragmented forests, interspersed with clearing and fields, whereas the latter has a clear preference for extensive primary or old secondary forest. A similar pattern is also present in Borneo between *S. cirrhatus* and *S. nanus* (V. Nijman, unpubl. data); habitat segregation between the two hawk-eagles on Java seems to be less well marked.

A predicted greater niche expansion of *S. bartelsi* as a result of a stronger effect of the insular syndrome on this endemic species compared with the wide-ranging *S. cirrhatus* was not supported by the data. The relative overlap between the two species on Java however may be influenced by current habitat types present on the island. Compared with the original dense, undisturbed primary forest, many present-day forest-like habitats have a rather open character or are disturbed. In more pristine conditions habitat segregation between the two

hawk-eagles might have been more clear-cut. Still, there was a segregation of habitats used, with *S. bartelsi* being essentially confined to the wetter closed-forest types and *S. cirrhatus* occurring largely in the more open habitat types, including those in areas with a marked dry season.

Altitudinal partitioning

Even at times when significantly more lowland forest remained than does at present, *S. bartelsi* was considered to have a preference for montane forests (Bartels 1924, Kuroda 1936), whereas *S. cirrhatus* has generally been associated with the lowlands (Bartels 1924, A. Hoogerwerf, unpubl. ms). In the present study *S. bartelsi* was recorded more often in the lowlands than in montane regions, but almost always in hilly or rugged terrain. Hitherto the species has not been recorded from the northern plains, although at present very little forest remains there. *Spizaetus bartelsi* may be a genuine slope species with special demands as to topographic relief (Janes 1985). Wells (1985) considered it a 'slope specialist', i.e. a species that is confined to the mountain slope fringe habitat between the lowland forest and the montane moss-forest ecotone, and that is altitudinally replaced by a congener (viz. *S. cirrhatus* or perhaps even another extinct hawk-eagle species: van Balen *et al*. 1999*b*). An alternative explanation for the more frequent recording of *S. bartelsi* in hill and montane habitats compared with lowland forests, favoured by H. Bartels (*pers. comm.*), is that the species is pushed into the hills because of the destruction of lowland forest. Since there is hardly any forest extant in the lowland plains on Java it is probably no longer possible to test these hypotheses. *Spizaetus cirrhatus* was more often recorded in lowland than in montane habitats and inhabited both mountainous terrain as well as the flat plains, and is restricted to areas below *c*. 1500 m asl.

In conclusion, the two congeneric hawk-eagles on Java are segregated by habitat, by topography of the terrain, and partially by altitude. There was no evidence for a broader habitat range in the endemic *S. bartelsi* compared with the wide-ranging *S. cirrhatus*, as found in two congeneric accipiters by Thiollay (1993). In fact, *S. bartelsi* occurred over a smaller range of habitats than *S. cirrhatus*. The once dense continuous rain forest has been fragmented into numerous small patches or has been replaced by more open habitat types. The initial expansion of available habitats for changeable hawk-eagles, at the cost of those of *S. bartelsi*, has been nullified by intensification of land use and increased persecution, which, in turn, may explain the small numbers of hawk-eagles recorded.

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