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Old World versus New World Long-Distance Migration in Accipiters, Buteos, and Falcons

*The Interplay of Migration Ability
and Global Biogeography*

WE EXPLORE HOW MIGRATION ABILITY affects Old versus New World distributions and abundances of species of raptors by comparing biogeography and species richness in three falconiform genera, *Accipiter*, *Buteo*, and *Falco*, that differ considerably in their migration abilities. Together, these three genera (*Accipiter*, 50 species; *Buteo*, 28; *Falco*, 37) comprise 37% of all birds of prey and 38% of all migratory raptors. Overall, *Accipiter*, *Buteo*, and *Falco* differ considerably in wing structure and aerodynamics and typically use different flight mechanics while migrating. These differences, in turn, are reflected in differences in both migration tendencies and behavior. More than 80% of all buteos and falcons are complete, partial, or irregular migrants, whereas only 40% of all accipiters migrate. In addition, buteos and falcons are more likely to be transequatorial, long-distance migrants than are accipiters. Accipiters tend to be more island restricted, forest dependent, range restricted, and wholly tropical than buteos and falcons. Island-restricted accipiters tend to occur on fringing archipelago islands more than on truly isolated oceanic islands, whereas island-restricted buteos and falcons occur on both types of islands. Buteos probably occur on isolated oceanic islands because they tend to be wind drifted while migrating in flocks; falcons, probably because of their considerable overwater flight abilities. The hourglass configuration of continental landmasses and the north-south orientation of mountain ranges in the New World are associated with long-distance *Buteo* migration and speciation there. The vast open habitats of sub-Saharan Africa are associated with long-distance falcon migration and speciation there. The largely forested, fringing archipelagos of

the South Pacific are associated with long-distance accipiter migration and speciation there. We describe a mechanism called “migration dosing” that we believe contributes to these relationships. Migration ability and continental geography are important emergent factors in determining Old versus New World patterns of raptor migration and species distribution.

INTRODUCTION

Migration abilities clearly affect the global distributions and abundances of birds. Several species of birds are naturally cosmopolitan, and many others have transcontinental distributions. Migration also has shaped the structures and relationships of regional avifaunas, including extensive large-scale, north-south relationships in both the Old and the New World (Darlington 1957; Snow 1978).

Although studies of avian migration and avian geography each have their own rich ornithological histories, investigations integrating these two important aspects of avian biology are generally lacking (see Brown and Lomolino 1998; Cox and Moore 2000; Mayr and Diamond 2001). To provide a framework for such studies, we explore how interactions between long-distance migration ability and global geography affect Old versus New World species distributions and abundances of the three most species-rich genera of diurnal birds of prey, *Accipiter*, *Buteo*, and *Falco*.

Raptors are ideal subjects for this study for several reasons. Falconiformes is one of the best-studied groups of birds, and its species geography and migration dynamics are reasonably well understood (Kerlinger 1989; Zalles and Bildstein 2000; Ferguson-Lees and Christie 2001). This group also exhibits a wide range of migration and dispersive behavior, including exceptional mobility that has produced some of the most capable and successful of all natural colonists (Stattersfield et al. 1998; Ferguson-Lees and Christie 2001).

METHODS

Taxonomy and Definitions

Taxonomy and common names follow del Hoyo et al. (1994). Migration is defined as directed, long-distance, recurring movement that alternates in direction and is temporally and spatially predictable. Complete migrants are species in which at least 90% of all individuals leave their breeding range during the nonbreeding season. Partial migrants are species in which fewer than 90% of all individuals migrate. Irruptive and irregular migrants are species whose migrations are less regular than those of complete and partial migrants (Kerlinger 1989). Migration geography largely follows Zalles and Bildstein (2000) and Ferguson-Lees and Christie (2001); flight strategies and mechanics follow Kerlinger (1989); ecology, distributions, and abundances largely follow Ferguson-Lees and Christie (2001).

Ecoregions used to describe principal flyways follow Bailey (1989). Endemism follows Stattersfield et al. (1998) (range-restricted) and Bildstein et al. (1998) (country and regional).

Study Genera

ACCIPITER. Accipiters are largely forest-dependent, woodland, and woodland-savanna raptors found on six continents and on numerous oceanic islands. Most accipiters are small- to medium-bodied “true hawks” with relatively short, rounded wings and longish tails; they range in size from 62-g (male) Tiny Hawks (*Accipiter superciliosus fontanieri*) to 2,200-g (female) Northern Goshawks (*A. g. gentilis*). A few, including all three long-distance migrants, have relatively long pointed wings and medium-length tails. With at least 50 species, *Accipiter* represents 21% of Accipitridae and 16% of Falconiformes and is the most species-rich of all raptor genera (Brown and Amadon 1968; Wattel 1973; Kerlinger 1989; del Hoyo et al. 1994; Ferguson-Lees and Christie 2001).

BUTEO. Buteos are largely savanna and open-habitat, and sometimes woodland and forest, raptors found on five continents (not including Australia) and on many oceanic islands. Buteos are small- to mostly medium-bodied “buzzards” with broad wings and tails; they range in size from 200-g (male) Roadside Hawks (*Buteo magnirostris nattereri*) to 2,050-g (female) Upland Buzzards (*B. hemilasius*). With at least 28 species, *Buteo* represents 12% of Accipitridae and 9% of Falconiformes (Brown and Amadon 1968; Kerlinger 1989; del Hoyo et al. 1994; Ferguson-Lees and Christie 2001).

FALCO. Falcons are largely open-habitat raptors found on six continents and numerous oceanic islands. Falcons are small to medium-bodied raptors, with long pointed wings and moderately long tails, that range in size from 62-g (male) Seychelles Kestrels (*Falco araea*) to 2,100-g (female) Gyrfalcons (*F. rusticolus*). With at least 37 species, *Falco* represents 61% of Falconidae and 12% of Falconiformes (Brown and Amadon 1968; Cade 1982; Kerlinger 1989; del Hoyo et al. 1994; Ferguson-Lees and Christie 2001).

RESULTS

Characteristics and Geography of Raptor Migration

At least 183 of the world’s 307 species of raptors migrate. Twenty species (7% of all raptors) are complete migrants (sensu Kerlinger 1989), 103 species (34%) are partial migrants, and 60 species (20%) are irruptive or local migrants (Zalles and Bildstein 2000). Most migration—particularly outside of the Tropics—is latitudinal (i.e., north-south). Raptors also migrate longitudinally (east-west) and altitudinally (Kerlinger 1989).

Raptors are lightly wing-loaded, and many species depend more heavily upon thermal- and slope-soaring to complete their migratory journeys than do many other species of birds (Brown and Amadon 1968; Kerlinger 1989; Berthold 2001). Most raptors migrate entirely by day, and most avoid long water crossings (Kerlinger 1989). A few species, including Levant Sparrowhawk (*Accipiter brevipes*), Amur Falcon (*Falco amurensis*), and Peregrine Falcon (*F. peregrinus*), migrate at night (Ferguson-Lees and Christie 2001). Although many raptors feed at least episodically when migrating, many larger species may forego eating for up to several weeks en route (Kerlinger 1989).

Both within and among species, migration tendencies increase with latitude, with high-latitude species that depend upon cold-blooded prey being particularly migratory. Overall, diurnal birds of prey are less migratory in the Southern than in the Northern Hemisphere (Kerlinger 1989); and, as is true for other groups of birds (Newton and Dale 1996), a lower percentage of raptors are migratory in Europe than in North America (Zalles and Bildstein 2000). Overall, 84 species migrate in Africa (61 excluding irruptive and local species); 75 (66) in mainland Asia, 45 (29) in South America, 44 (33) in North America, 39 (29) in the Pacific Islands, 38 (38) in Europe, and 22 (11) in Australia (Zalles and Bildstein 2000).

For at least portions of their migrations, most raptors migrate across broad fronts (Bednarz and Kerlinger 1989). Many species also engage in considerable small- or narrow-front migration (sensu Berthold 2001), usually along well-established migration corridors. Corridors typically occur along landscape features that include mountain ranges, river valleys, coastlines, and habitat discontinuities that act as "leading lines" (sensu Geyr von Schweppenburg 1963:192) to migration (Zalles and Bildstein 2000). Most corridors coalesce into one of five principal migration flyways, four of which are transequatorial (fig. 13.1). The main intercontinental flyways converge on narrow land bridges (such as Panama or Suez), or short water crossings (such as

Gibraltar). Descriptions of these flyways, and the migrants that use them, follow.

TRANSAMERICAN FLYWAY. Each autumn, more than 5 million raptors travel along this 10,000-km overland system of corridors that stretches from central Canada to central Argentina (fig. 13.1). At least 32 species, including three accipiters, eight buteos, and five falcons, migrate along the flyway's central portion, the 4,000-km Mesoamerican Land Corridor, which connects North and South America. The bulk of the long-distance, transequatorial flight is dominated by world populations of Mississippi Kites (*Ictinia mississippiensis*), Broad-winged Hawks (*Buteo platypterus*), and Swainson's Hawks (*B. swainsoni*) and western North American breeding populations of Turkey Vultures (*Cathartes aura*) (Bildstein and Zalles 2000). Additional long-distance migrants include Rough-legged Hawks (*B. lagopus*) (northern third of the flyway only), Merlins (*Falco columbarius*), and Peregrine Falcons. No long-distance accipiter migrants use the flyway (fig. 13.2).

North to south, the Transamerican Flyway is tundra, mixed coniferous-deciduous forest, humid broad-leaved forest, steppe, dry steppe and shrub savanna, a mosaic of savanna, open woodland shrub, humid deciduous mixed forests, a mosaic of mixed rainforest and savanna, and steppe (Bailey 1989).

WESTERN EUROPEAN–WEST AFRICAN FLYWAY. Each autumn, approximately 200,000 raptors travel along the 5000-km overland system of corridors that stretches from Scandinavia to West Africa (fig. 13.1). At least 22 species, including two accipiters, two buteos, and five falcons, fly between western Europe and Africa along this flyway, which includes a short (<14-km) water crossing at the Strait of Gibraltar. The bulk of the long-distance flight is dominated by European breeding populations of Western Honey-buzzards (*Pernis apivorus*) and Black Kites (*Milvus migrans*). Additional long-distance migrants include Rough-legged

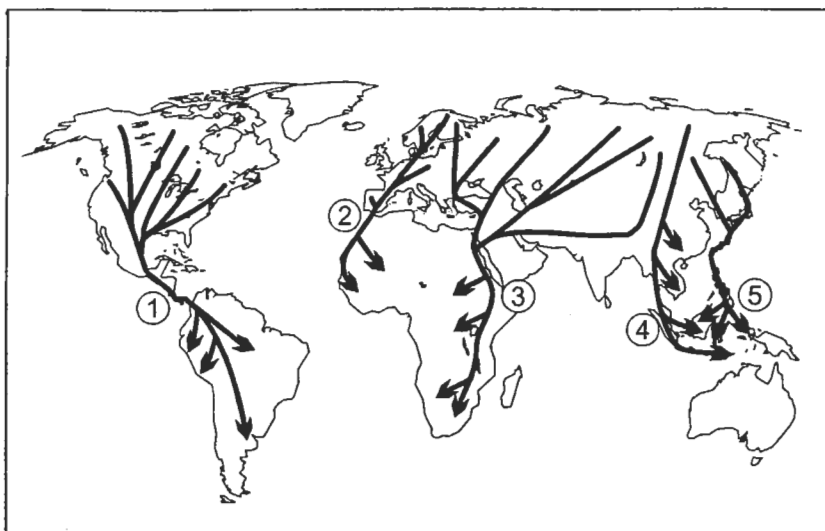


Fig. 13.1. Principal flyways used by accipiters, buteos, and falcons: (1) Transamerican Flyway, (2) Western–European–West African Flyway, (3) Eurasian–East African Flyway, (4) East Asian Continental Flyway, and (5) East Asian Oceanic Flyway. (See text for details.)

Hawks (northern third of the flyway only), Merlins (northern half of the flyway only), Northern Hobbies (*Falco subbuteo*), and Peregrine Falcons. No long-distance accipiter migrants use the flyway (fig. 13.2).

North to south, the Western European–West African Flyway is tundra, coniferous or deciduous forest, Mediterranean scrub and desert, desert, arid scrub, and woodland savanna and rainforest (Bailey 1989).

EURASIAN–EAST AFRICAN FLYWAY. More than 1.5 million raptors travel along this 10,000-km system of largely overland corridors that stretches from eastern Scandinavia and western Siberia through the Middle East into southern Africa (fig. 13.1). At least 35 species, including three accipiters, three buteos, and nine falcons, use the flyway that follows the course of the Great Rift Valley and includes narrow water crossings at the Bosphorus, Sinai Peninsula, and Babel-Mandeb Straits. Six Palearctic breeders, the Western Honey-buzzard, Black Kite, Levant Sparrowhawk, Eurasian (Steppe) Buzzard (*Buteo buteo vulpinus*), Lesser Spotted Eagle (*Aquila pomarina*), and Steppe Eagle (*A. nipalensis*), make up the bulk of the flight through the Middle Eastern part of the flyway. Additional long-distance migrants include Rough-legged Hawks (northern third of the flyway only), Lesser Kestrels (*Falco naumanni*), Western Red-footed Falcons (*F. vespertinus*), Merlins, Northern Hobbies, and Peregrine Falcons (fig. 13.2). The Amur Falcon may use portions of the flyway in spring.

North to south, the Eurasian–East African Flyway is tundra, coniferous forest, steppe, Mediterranean scrub and desert, woodland savanna, and a mosaic of open and closed woodland savanna (Bailey 1989).

EAST ASIAN CONTINENTAL FLYWAY. More than 1 million raptors travel along this 7,000-km mostly overland system of corridors that stretches from eastern Siberia to Southeast Asia and the Indonesian Archipelago, and that includes water crossings of 25–60 km at the Straits of Malacca, Sunda, Bali, and Lombok (fig. 13.1). At least 33 species, including four accipiters, three buteos, and seven falcons, migrate along portions of the flyway through eastern Asia. The bulk of the long-distance flight is dominated by Palearctic populations of Crested Honey-buzzards (*Pernis ptilorhynchus*), Grey-faced Buzzards (*Butastur indicus*), and Japanese Sparrowhawks (*Accipiter gularis*). Eurasian Buzzards (*B. b. japonicus*) migrate in the northern half of the flyway. Additional long-distance migrants include Rough-legged Hawks (northern third of the flyway only), Amur Falcons, Merlins, Northern Hobbies, and Peregrine Falcons (fig. 13.2).

North to south, this largely overland flyway is tundra, coniferous forest, steppe, desert and steppe or deciduous forest, and tropical rainforest with some savanna (Bailey 1989).

EAST ASIAN OCEANIC FLYWAY. As many as 150,000 to 500,000 raptors travel along this 5000-km, mostly overwater

route that stretches from coastal eastern Siberia and Kamchatka to Japan, the Philippines, and into eastern Indonesia (fig. 13.1). At least 19 species, including four accipiters, two buteos, and four falcons, migrate along the flyway's main corridor, which extends from southern Japan through the Ryukyu Islands and Taiwan to the Philippines and eastern Indonesia. The bulk of the long-distance flight is dominated by Grey-faced Buzzards and Chinese Goshawks (*A. soloensis*). Additional long-distance migrants include Rough-legged Hawks (northern third of the flyway only), Eurasian Buzzards, Merlins, Northern Hobbies, and Peregrine Falcons (fig. 13.2). Long water crossings may restrict the numbers and variety of species that use this flyway.

North to south, the flyway is tundra, coniferous forest, deciduous forest, and tropical rainforest, interspersed throughout with short to long water crossings of up to 300 km (Bailey 1989).

Differences in the Migration Tendencies of *Accipiter*, *Buteo*, and *Falco*

Differences in the migration tendencies of accipiters, buteos, and falcons generally reflect anatomical differences among the three groups. Accipiters tend to have relatively short, rounded wings and long, narrow tails, whereas buteos have broad wings with considerable wing slotting, and relatively short, broad tails. Falcons have relatively long, high-aspect-ratio, pointed wings and longish tails (Kerlinger 1989). As a result, buteos are largely thermal- and slope-soaring migrants, whereas falcons are largely powered-flight migrants. Accipiters fall in between buteos and falcons in their use of soaring versus powered flight during migration.

Although thermal- and slope-soaring are difficult to achieve over water, direct, powered flight is particularly well suited for such travel, especially on tailwinds and crosswinds. As a result, buteos rarely undertake lengthy overwater crossings on migration, whereas falcons frequently do so.

Members of all three genera feed on migration. Accipiters and falcons tend to do so regularly, whereas buteos feed more episodically. All long-distance *Buteo* migrants and most, if not all, long-distance *Accipiter* migrants flock on migration, whereas only about half of the long-distance *Falco* migrants flock regularly (Kerlinger 1989; Zalles and Bildstein 2000; Ferguson-Lees and Christie 2001) (see table 13.1 and the Appendix to this chapter).

ACCIPITER. With only two complete migrants (4% of all accipiters) and 13 (26%) partial migrants, accipiters are one of the least migratory of all raptor genera (table 13.1). Most migrants in the genus, including the Western Hemisphere Sharp-shinned Hawk (*Accipiter striatus*), North American Cooper's Hawk (*A. cooperii*), Eurasian Shikra (*A. badius*), and Eurasian Sparrowhawk (*A. nisus*), are continentally based, short- and medium-distance, partial migrants that use undulating or flap-glide flight (*sensu* Kerlinger

Fig: 13.2. Long-distance migration in accipiters (A), buteos (B), and falcons (C). Numbers refer to principal routes used by long-distance migrants.

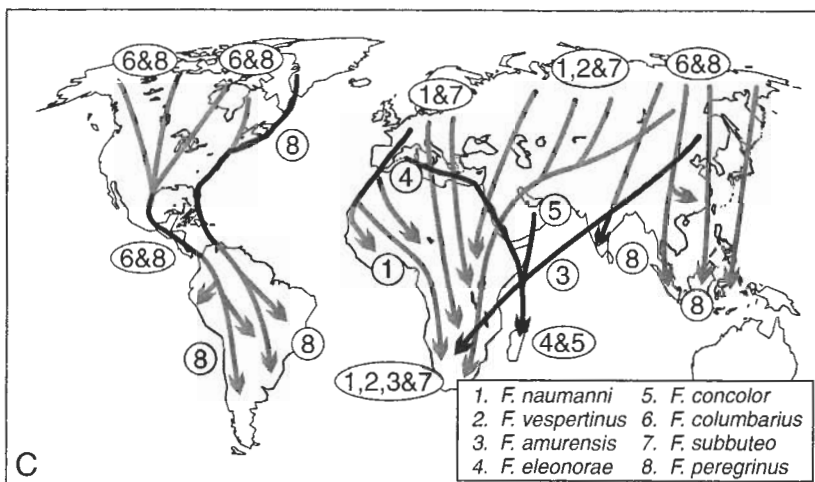
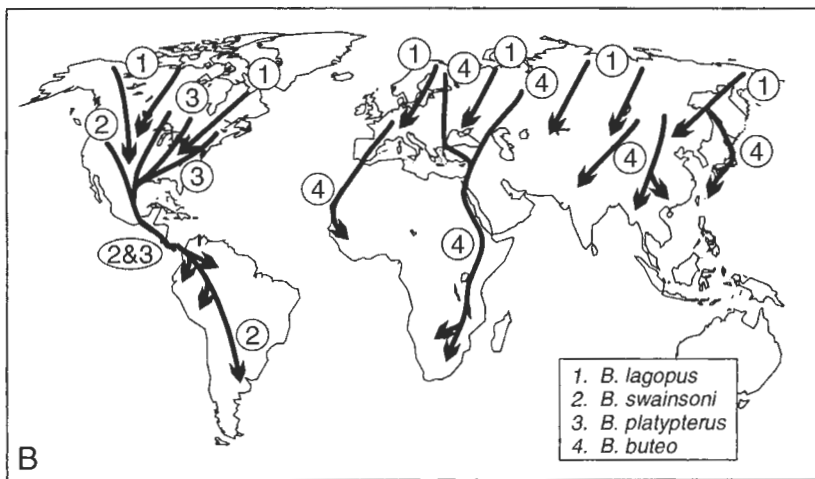
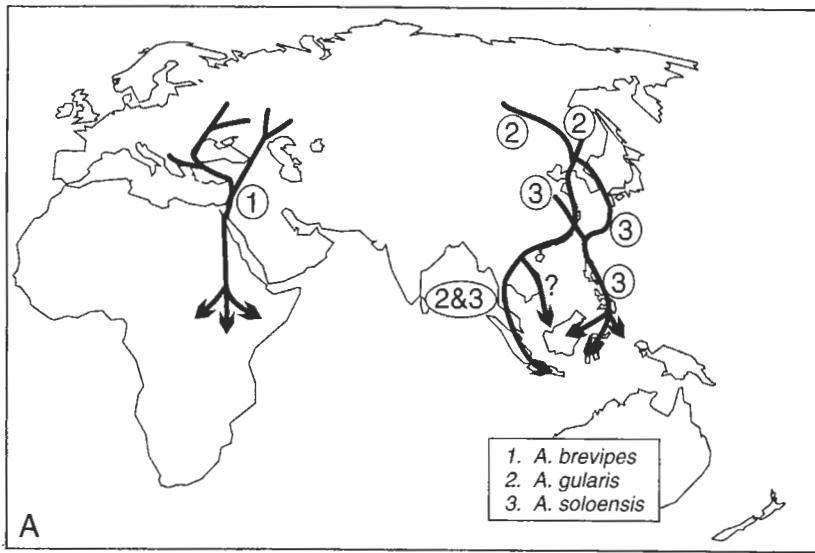


Table 13.1 Migration characteristics of *Accipiter*, *Buteo*, and *Falco*

Number of species (%)	<i>Accipiter</i>	<i>Buteo</i>	<i>Falco</i>
Total in genus ^a	50	28	37
Migratory ^b	20 (40%)	25 (89%)	30 (81%)
Complete migrants ^b	2 (4%)	3 (11%)	6 (16%)
Partial migrants ^b	13 (26%)	14 (50%)	17 (46%)
Irruptive or irregular migrants ^b	5 (10%)	8 (29%)	7 (19%)
Long-distance migrants ^c	3 (6%)	4 (14%)	9 (24%)
Transequatorial migrants ^d	2 (4%)	3 (11%)	7 (19%)
Intermediate-water-crossing species ^e	3 (6%)	1 (4%)	8 (22%)
Long-water-crossing species ^e	1 (2%)	0 (0%)	8 (22%)
Flocking migrants ^f	3 (6%)	4 (14%)	6 (16%)
Old World species	39 (78%)	9 (32%)	29 (78%)
New World species	10 (20%)	17 (61%)	5 (14%)
Cosmopolitan species	1 (2%)	1 (4%)	4 (11%)
Wholly tropical species	25 (50%)	5 (18%)	5 (14%)
Island-restricted species ^g	21 (42%)	4 (14%)	6 (16%)
Restricted-range endemics ^h	11 (22%)	4 (14%)	2 (5%)
Country endemics ⁱ	9 (18%)	1 (4%)	6 (16%)

^aTaxonomy based on del Hoyo et al. 1994.

^bAll migratory species, including complete migrants (species in which >90% of all individuals leave the breeding range outside of the breeding season), partial migrants (species in which ≤90% of all individuals leave the breeding range), and irruptive and irregular migrants (species whose movements are less regular than the above) (sensu Zalles and Bildstein 2000).

^cSpecies in which more than 20% of all individuals (sometimes entire subspecies) regularly migrate more than 1,500 km.

^dLong-distance migrants in which more than 20% of all individuals (sometimes entire subspecies) regularly migrate across the equator.

^eSpecies that regularly undertake intermediate (25–100 km) or long (>100 km) water crossings during migration (as updated from Kerlinger 1989).

^fSpecies that regularly migrate in flocks.

^gSpecies found only on islands (including continental islands, oceanic islands, and archipelagos).

^hSpecies whose historic and current breeding ranges are larger than 50,000 km² (based on Stattersfield et al. 1998).

ⁱSpecies whose historic and current breeding ranges although restricted to a single country are larger than 50,000 km².

1989) interrupted by slope-soaring while migrating alone and in small groups of from two to six birds (Appendix to this chapter). Most accipiters appear to feed regularly en route (Shelley and Benz 1985), often on migrating passerines (Belopolski 1971; Rosenfield and Bielefeldt 1993; McCanch 1997; Bildstein and Meyer 2000).

Unlike “typical” *Accipiter* migrants, three Old World species, the Levant Sparrowhawk (*A. brevipes*), Chinese Goshawk (*A. soloensis*), and Japanese Sparrowhawk (*A. gularis*), are highly synchronous, gregarious long-distance migrants that sometimes travel in flocks of more than 1,000 birds (Appendix to this chapter).

Both the Japanese Sparrowhawk and Chinese Goshawk are transequatorial migrants. The Levant Sparrowhawk engages in considerable thermal soaring and nocturnal flapping flight (Stark and Liechti 1993; Shirihai et al. 2000). The Chinese Goshawk and the Japanese Sparrowhawk probably do so as well.

The Japanese Sparrowhawk, which migrates along the East Asian Continental Flyway, undertakes several over-

water passages of more than 25 km in southern Malaysia and western and central Indonesia en route (fig. 13.2). The Chinese Goshawk also migrates along this flyway, as well as along the East Asian Oceanic Flyway, where it makes numerous water crossings of 300 km or less (fig. 13.2). Both species presumably fuel the undulating-flight portions of their migrations with a combination of preflight fat deposition and, at least for the Japanese Sparrowhawk, considerable feeding en route.

The only other long-distance accipiter migrant, the Levant Sparrowhawk, uses northern and central portions of the Eurasian–East African Flyway. This species, which occurs primarily in mixed and open habitats, is similar to the Chinese Goshawk in having long, pointed wings and shortish tails. Both species migrate synchronously and frequently in large soaring flocks (Shirihai et al. 2000). The Levant Sparrowhawk presumably manages to complete its 5,000- to 6,000-km journey across considerable inhospitable desert with a combination of solar-powered soaring flight and fat-powered undulating flight.

BUTEO. With three complete migrants (11% of all buteos) and 14 (50%) partial migrants, buteos are one of the most migratory of all raptor genera (table 13.1). Most migratory buteos, including the Red-tailed Hawk (*B. jamaicensis*) and nominate race of the Eurasian Common Buzzard (*B. b. buteo*), are short- to medium-distance, partial migrants that rely heavily upon both slope- and thermal-soaring to complete their migrations. Most travel alone or in small groups of up to ten birds (Appendix to this chapter). Although some feed regularly en route, others appear to do so only opportunistically.

Long-distance migrants in the group include the New World Broad-winged Hawk (*B. platypterus*) and Swainson's Hawk (*B. swainsoni*), the circumboreal Rough-legged Hawk (*B. lagopus*), the northernmost race of the Eurasian (Steppe) Buzzard (*B. b. vulpinus*), and an East Asian, *japonicus*, race of the Eurasian Buzzard (Appendix to this chapter).

Three of these, the Broad-winged Hawk, Swainson's Hawk, and Steppe Buzzard, are transequatorial migrants that depend on soaring flight to complete their journeys (Bildstein 1999). All three rarely undertake all but the shortest overwater crossings (Goodrich et al. 1996; England et al. 1997; Spaar and Bruderer 1997), and all three migrate only along flyways that are exclusively overland (or nearly so) with considerable open habitats (fig. 13.2). Broad-winged and Swainson's Hawks migrate along the overland Trans-american Flyway; the Steppe Buzzard migrates along the Eurasian–East African Flyway (Bildstein and Zalles 2001; Ferguson-Lees and Christie 2001) (fig. 13.2). *Buteo b. japonicus* migrates between northeastern and southeastern Asia along northern portions of the East Asian Continental Flyway, but not along the flyway's southern half, where passage would require water crossings of more than 25 km. *Japonicus* also migrates along the northern, largely overland portion of the East Asian Oceanic Flyway, but only irregularly farther south, where passage would require even longer water crossings.

All long-distance *Buteo* movements involve prolonged passage over desert or steppe, during which the birds soar almost exclusively, and all three transequatorial migrants overwinter in open habitats or in mosaics of open habitat and forest (see Bailey 1989; Ferguson-Lees and Christie 2001).

FALCO. With six complete migrants (16% of all falcons) and 17 (46%) partial migrants, *Falco* also is one of the most migratory of all raptor genera (table 13.1). Many migratory falcons, including the circumboreal Merlin, cosmopolitan Peregrine Falcon, Western Hemisphere American Kestrel (*F. sparverius*), Old World Saker Falcon (*F. cherrug*), and Eurasian Kestrel (*F. tinnunculus*), are short- to medium-distance migrants that travel alone or in small groups and rely on a combination of powered flight and feeding en route to complete their migrations.

Seven species of falcons undertake long-distance transequatorial migrations. Three of these, the Old World Lesser

Kestrel, Northern Hobby, and Amur Falcon, are synchronous and moderately to highly gregarious migrants. Two additional species make long-distance movements entirely within the Northern Hemisphere.

Unlike buteos and accipiters, whose long-distance migrations are largely constrained by the presence of continental land masses and archipelagos, six of the seven transequatorial *Falco* migrants (Appendix to this chapter) fly long distances (i.e., >100 km) over open water when traveling between breeding and wintering areas. One species, *amurensis*, undertakes the longest regular overwater passage of any raptor, a crossing of the Indian Ocean of more than 4,000 km between southwestern India and tropical East Africa that includes nocturnal flight. This species, which breeds in central to northeastern Asia and overwinters in East Africa, first travels south to northeastern India and Bangladesh, where it apparently fattens (Ali and Ripley 1978) while staging for overland and then overwater flights across peninsular India and the Indian Ocean, respectively. The latter passage, which occurs in late November–early December, is assisted by northern-winter monsoonal tail winds, which are then in place. The species is an elliptical migrant (sensu Kerlinger 1989), and its return migration in spring occurs largely overland north and west of its outbound passage.

Eleonora's Falcon (*F. eleonora*), which breeds in the Mediterranean Basin and overwinters in Madagascar, is another exceptional migrant. Rather than flying overland across Africa, most *eleonora* migrate east, along the Mediterranean, and then south along the Red Sea, before "shortcutting" inland across Somalia to avoid circumnavigating the Horn of Africa. They then continue south along the coast of East Africa. The species presumably feeds en route.

All nine long-distance migratory falcons have been recorded at watchsites along at least one of the world's principal raptor flyways, and two species (*columbarius* and *peregrinus*) have been recorded at watchsites along all five flyways. Even so, falcons appear to be far less constrained by continental geography than accipiters and buteos (fig. 13.2).

Relationships between Migration Geography and Endemism

ACCIPITER. Two accipiters, the Japanese Sparrowhawk and Chinese Goshawk, are long-distance, transequatorial migrants. Both overwinter in Southeast Asia and on islands in the South Pacific Ocean and Andaman Sea. All 11 range-restricted endemic accipiters (Stattersfield et al. 1998) also occur in the region, and 10 of the 11 are restricted to areas east of Wallace's Line. The only range-restricted endemic west of Wallace's Line, the Nicobar Sparrowhawk (*A. butleri*), is generally considered an allospecies of the highly migratory Chinese Goshawk. Many of the remaining endemics differ considerably among themselves in plumage, size, and wing formulae (Wattel 1973), and some are considered allospecies of several superspecies. At least some of

these endemics appear to have speciated via mechanisms suggested for many of the birds in the region (see Mayr and Diamond 2001). Of the nine country endemics (Appendix to this chapter), five are from this region, compared with three from Africa and one from Central and South America.

BUTEO. Three buteos, Broad-winged Hawk, Swainson's Hawk, and Steppe Buzzard, are long-distance, transequatorial migrants. The first two overwinter in Central and South America, and the third overwinters in Africa. Three of four range-restricted endemics in the genus, Galapagos Hawk (*B. galapagoensis*), Ridgway's Hawk (*B. ridgwayi*), and Archer's Buzzard (*B. archeri*), also occur in these regions. The fourth range-restricted endemic is the Hawaiian Hawk (*B. solitarius*). Mayr (1943) initially described the Hawaiian Hawk as a geographic representative of *swainsoni* as well, and two molecular phylogenies indicate that *solitarius* forms a clade with both *galapagoensis* and *swainsoni*, as well as with the Central and South American Short-tailed Hawk (*B. brachyurus* [Fleischer and McIntosh 2001; Riesing et al. 2003]). The only country endemic is the Madagascar Buzzard (*B. brachypterus*) (fig. 13.2).

FALCO. Seven *Falco* species, *naumanni*, *vespertinus*, *amurensis*, *eleonora*, *concolor*, *subbuteo*, and *peregrinus*, are long-distance, transequatorial migrants. The first three overwinter exclusively or almost exclusively in Africa, the fourth in Madagascar, the fifth in both Africa and Madagascar, and the sixth in Africa and southern Asia. *Peregrinus* overwinters throughout the Southern Hemisphere. All seven species occur along the world's major flyways. However, many are broad frontal migrants that engage in long-distance water crossings. *Falco* has two range-restricted endemics, *punctatus* and *araea*, and six country endemics, *newtoni*, *moluccensis*, *zoniventris*, *hypoleucos*, *novaeseelandiae*, and *subniger*. Four of these are Malagasy, one is Moluccan, two are Australian, and one is from New Zealand.

DISCUSSION

Our analyses demonstrate clear and consistent differences in the global geography of long-distance migration in *Accipiter*, *Buteo*, and *Falco*, most, if not all, of which can be ascribed to intergeneric differences in migration ability. They also reveal substantial linkages between migration patterns and centers of endemism in each of the three genera (fig. 13.2).

In the New World, the hourglass configuration of continental landmasses, together with the north-south orientation of mountain ranges, has created opportunities for long-distance soaring migration and speciation in buteos. In sub-Saharan Africa, the vast open habitats are associated with long-distance falcon migration and speciation. And the largely forested, fringing archipelagos of the South Pacific region are associated with long-distance accipiter migration and speciation in this part of the world.

Taken together, these relationships suggest that long-distance migration ability and continental-scale geography and ecology are important determinants in migration geography and patterns of species distributions in raptors. Below we describe a speciation mechanism we call "migration dosing" that we believe contributes to species distribution in raptors, and we discuss this mechanism in terms of global biodiversity and conservation biology.

MIGRATION DOSING AND RAPTOR SPECIATION.

One of the unintended consequences of large-scale post-breeding raptor migration is that each year some of the migrants, particularly inexperienced juveniles (Agostini and Logozzo 1995; Agostini et al. 2002; Hake et al. 2003; Thorup et al. 2003), are diverted from their principal migration routes, either by weather or by failed navigational systems. Once displaced, some of the misguided migrants are likely to wind up in areas that are geographically isolated from the species' traditional wintering areas. These vagrants (sensu Newton 2003) face three potential outcomes: death in the new-found area before breeding, successful reorientation and subsequent return to the breeding grounds in spring, or, along with other simultaneously diverted vagrants, successful breeding in the new area. The last possibility results in migration dosing.

As we see it, migration dosing is orchestrated vagrancy that occurs when "doses" of potential colonists in the form of diverted long-distance migrants: (1) simultaneously arrive in areas tangential to or beyond their major migration flyways, (2) subsequently fail to return to their normal destinations the following season, and (3) eventually speciate in isolation. For speciation to occur via this mechanism, dosing must be highly irregular and must occur at well-spaced intervals. Most likely, inexperienced juveniles constitute the majority of "dosed" propagules, as they often travel together, are especially prone to wind drift (Kerlinger 1989; Hake et al. 2003; Thorup et al. 2003), have a higher likelihood of developing new migratory habits (Viverette et al. 1996), and, for some species, are less likely than adults to leave overwintering areas the following spring (Ferguson-Lees and Christie 2001).

Unlike *adaptive radiation*, which involves the "simultaneous divergence of numerous lines from much the same adaptive type into different [and] also diverging adaptive zones" (Simpson 1953), migration dosing refers to changes from relatively *specialized* highly migratory continental forms into other specialized or, in some instances, *generalized* sedentary insular or continental forms. (See Brown and Kodric-Brown 1977, Snow 1978, and Hubbell 2001 for arguments supporting aspects of this type of speciation mechanism, and Grinnell 1922 for the role that accidentals or vagrants can play in avian biogeography.)

Although the phenomenon of migration dosing has yet to be appreciated as a speciation mechanism, conditions favoring it, including long-distance movements, migration in large flocks, vulnerability to wind drift, and high rates of va-

grancy among migratory birds (Alerstam 1990; Newton 2003), as well as numerous examples of speciation that are most simply explained by this process, are widespread in the avian literature (Snow 1978; Bildstein 2004).

Long-distance, transequatorial migratory raptors are ideal candidates for migration dosing for several reasons. Most prey on resources that are "nutritionally substitutable," rather than on specific taxa, and this, together with the reduced intraguild predation and interference competition they are likely to encounter on most isolated islands, enhances the likelihood of groups of founders surviving there (Pimm 1991; Schuler 2000; Blackburn and Duncan 2001). Also, many raptors soar on migration, increasing the chance of "wind drift" en route, particularly among first-year birds (Kerlinger 1989), and especially within the tropical-cyclone regions that most transequatorial migrants travel through (NOAA 1988). Finally, most long-distance migrants travel in large flocks, substantially increasing the likelihood of simultaneous mis-transport of potential colonizing propagules (Williamson 1996).

Although migration dosing most likely occurs when raptors are blown off course and onto relatively isolated islands from which return may be difficult, we believe that it also happens on continental land masses when selection favors the elimination of migration behavior among certain populations of migratory species. This would include situations in which extrinsic environmental change or growing population densities within traditional breeding areas select against existing migration strategies (Berthold 1999).

Having established a theoretical framework for migration dosing, we now provide evidence to support its occurrence in *Accipiter*, *Buteo*, and *Falco*. The most detailed analysis of geographical differentiation in *Accipiter* concludes that the genus originated in Eurasia and spread from there (Wat-

tel 1973). If this is true, then the most likely route of accipiter colonization in the South Pacific would be from northwest to southeast (i.e., from continental Asia outward across Pacific archipelagos). Although some might suggest that "faunal dominance" (sensu Mayr and Diamond 2001), together with the archipelago nature of the region, is responsible for the origin and distribution of the large number of *Accipiter* species in the South Pacific (fig. 13.3), we suggest that migration dosing also has played an important role in speciation events there.

Each autumn, more than 400,000 Chinese Goshawks and about 100,000 Japanese Sparrowhawks (Ferguson-Lees and Christie 2001; Chong 2000) migrate along the East Asian Continental and Oceanic Flyways into peninsular Malaysia, the Philippines, the Indonesian Archipelago, and their geographically associated islands. Both species, and in particular *soloensis*, often travel in multithousand-bird flocks. In most years, both species complete their southbound journeys in autumn with the aid of seasonal monsoonal northwesterly winds, and their northwesterly springtime returns are aided by easterly trade winds (Lam and Williams 1994; Krishnamurti 1996). Each autumn, however, their migrations take them through an active tropical-cyclone region (NOAA 1988), and during the springs of El Niño–Southern Oscillation events, strong westerly winds replace the region's easterly trade winds (Glantz 2001).

We suggest that migration geography and climatic conditions such as these provide the backdrop for infrequent but inevitable episodes of misdirected migrations during which flocks of *gularis* and *soloensis* are blown off course and onto islands in the region's archipelagos from which, because of adverse winds, they are unable to return to their breeding grounds. These dosed propagules then provide potential seed stock for regional endemism.

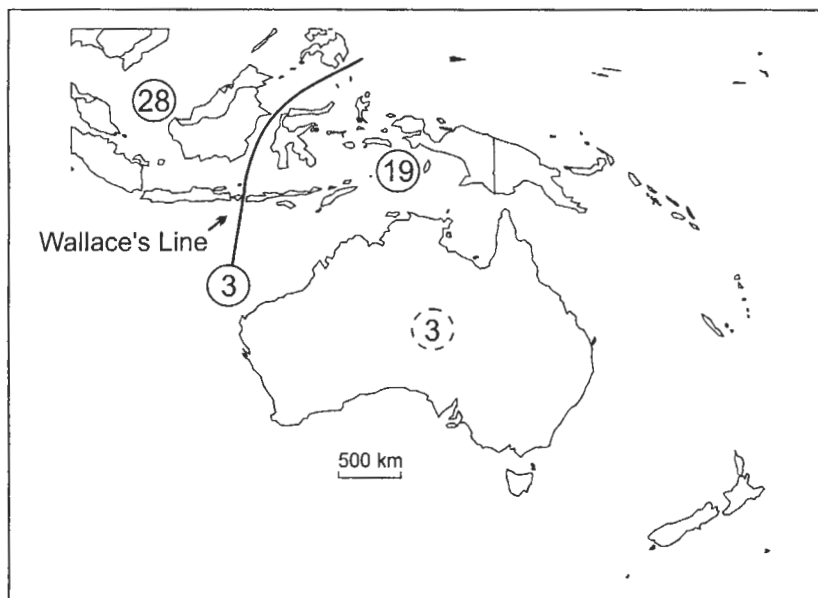


Fig. 13.3. Global distribution of the world's 50 species of accipiters relative to Wallace's Line. Twenty-eight species occur either only in the New World or west of Wallace's Line in the Old World, or both. Nineteen species occur only east of Wallace's Line, either in Wallacea or in Australasia, and three of these occur only in Australia. Three additional species occur on both sides of the line.

That migration dosing has contributed to the high-level *Accipiter* endemism in the region is supported by the coincidental lack of long-distance *Buteo* migration and endemism there, as well as by the relative paucity of long-distance *Accipiter* migration and endemism elsewhere in the world (figs. 13.2, 13.3). We do not claim that all or even most of the region's endemic accipiters resulted directly from migration dosing. Two of the region's endemics, the Nicobar Sparrowhawk and the Sulawesi Dwarf Sparrowhawk (*A. nanus*), however, almost certainly have resulted from this mechanism (see Ferguson-Lees and Christie 2001).

An additional example of migration dosing in *Accipiter* includes three Central and South American species (*chionogaster*, *ventralis*, and *erythronemius*) that are often considered allospecies of the partially migratory North American Sharp-shinned Hawk (*A. striatus*), a species that regularly migrates into Mexico and northern Central America (Ferguson-Lees and Christie 2001).

Examples of migration dosing in *Buteo* include the range-restricted endemic Galapagos Hawk and, possibly, Hawaiian Hawk, both of which are closely related to the highly migratory Swainson's Hawk (Riesing et al. 2003). *Falco* examples include the Oriental Hobby (*F. severus*) and the Australian Hobby (*F. longipennis*), which often are considered allospecies of the highly migratory Northern Hobby.

At the subspecies level, five nonmigratory Caribbean races of the Broad-winged Hawk, *B. platypterus* (*cubanensis*, *brunnescens*, *insulicola*, *rivierei*, *antillarum*), and six races of the Eurasian Buzzard (*bannermani* [Cape Verdes], *insularum* [Canaries], *rothschildi* [Azores], *arrigonii* [Corsica-Sardinia], *toyoshimai* [Izu and Bonin Islands], and *oshiroi* [Daito-jima]), occur on islands that are along or at the ends of migration flyways regularly used by these migratory buteos. Similarly, four nonmigratory, insular endemic subspecies of the Eurasian Kestrel (*canariensis* [Madeira and western Canary Islands], *dacotiae* [eastern Canaries], *neglectus*, [northern Cape Verde Island], and *alexandri* [southeast Cape Verde]), as well as four Caribbean races of the American Kestrel (*sparveroides*, *dominicensis*, *brevipennis*, and *caribaeorum*) occur on islands along or near the ends of major migration corridors for these species.

Although it is possible that these insular subspecies represent examples of incipient migration-dosed speciation, we believe that they more likely reflect circumstances in which extensive and regular migratory intrusions by continental propagules act to prevent speciation (Brown and Kodric-Brown 1977). (See Rowlett 1980 and Hagar 1988 for why the latter may be true for *platypterus*.)

CONCLUSIONS AND FUTURE DIRECTIONS

Our comparisons of the migration abilities and species geography in *Accipiter*, *Buteo*, and *Falco* demonstrate substantial linkages between the two phenomena. Within these three groups of birds of prey, differences in long-distance migration ability appear to have shaped regional, continental, and global patterns of species richness. In fact, we suggest that migration ability and its potential for colonization events via *migration dosing* explains regional differences in species richness in the three groups at least as well as do regional differences in ecological resources and ecosystem function. This latter point has important implications for conservation biology.

Although conservation biologists continue to focus considerable attention on describing and protecting biological diversity at various geographic scales, the discipline remains remarkably ignorant of the natural forces that shape and maintain such diversity (Hubbell 2001). This ignorance continues to compromise our ability to protect existing levels of biological diversity as well as to reconstruct historic levels. To date, most investigations regarding the creation and maintenance of natural biological diversity have centered on the roles that local and regional resource availability, geography, ecosystem process, and dispersal play in shaping that diversity (see Gaston 2000, Primack 2002). In contrast, little if any attention has been paid to the role that long-distance migration might play in creating and maintaining geographic patterns of biological diversity.

Our findings suggest that migration plays an important role in shaping patterns of species richness in several genera of Falconiformes. It seems reasonable to conclude that the associations we have uncovered in raptors also may occur in other groups of birds, and we advocate investigating this possibility. Specifically, we recommend that researchers examine whether long-distance flocking migrants are more likely than nonflocking migrants and nonmigrants to have closely related insular and endemic continental forms and, if so, whether such forms are more likely to occur along and beyond the principal migration routes of the migrants in question. We also recommend that systematists working on molecular phylogenies consider migration dosing when assessing the relationships they uncover. Finally, we recommend that migration dosing also be considered when researchers attempt to explain geographic patterns of species diversity in other groups of migratory animals, including insects. We think that such investigations will yield valuable insights into the creation and maintenance of species diversity, and should improve our ability to protect that diversity.

APPENDIX: MIGRATION CHARACTERISTICS OF INDIVIDUAL SPECIES OF ACCIPITER, BUTEO, AND FALCO

Species	Type migrant ^a	Long-distance migrant ^b	Trans-equatorial migrant ^c	Water crossing behavior ^d	Flocking behavior ^e	World distribution ^f	Wholly tropical species ^g	Island-restricted species ^h	Endemic species ⁱ
<i>Accipiter</i>									
<i>poliogaster</i>	P	N	N	N	N	NW	N	N	N
<i>trivirgatus</i>	I			N	N	OW	N	N	N
<i>griseiceps</i>	NM					OW	Y	Y	CE
<i>toussenelii</i>	NM					OW	Y	N	N
<i>tachiro</i>	I			N	N	OW	N	N	N
<i>castanilius</i>	NM					OW	Y	N	N
<i>badius</i>	P	N	N	N	N	OW	N	N	N
<i>butleri</i>	NM					OW	Y	Y	RRS
<i>brevipes</i>	C	Y	N	I	R(>1000)	OW	N	N	N
<i>soloensis</i>	C	Y	Y	L	R(>100)	OW	N	N	N
<i>francesii</i>	NM					OW	N	Y	CE
<i>trinotatus</i>	NM					OW	Y	Y	CE
<i>novaeollandiae</i>	NM					OW	N	N	N
<i>fasciatus</i>	P	N	N	I	N	OW	N	N	N
<i>melanochlamys</i>	NM					OW	Y	Y	CE
<i>albugularis</i>	NM					OW	Y	Y	RRS
<i>haplochrous</i>	NM					OW	Y	Y	RRS
<i>rufitorques</i>	NM					OW	Y	Y	RRS
<i>henicogrammus</i>	NM					OW	Y	Y	RRS
<i>luteoschistaceus</i>	NM					OW	Y	Y	RRS
<i>imitator</i>	NM					OW	Y	Y	RRS
<i>poliocephalus</i>	NM					OW	Y	Y	CE
<i>princeps</i>	NM					OW	Y	Y	RRS
<i>superciliosus</i>	NM					OW	N	N	N
<i>collaris</i>	NM					NW	Y	N	N
<i>erythropus</i>	NM					OW	Y	N	N
<i>minullus</i>	I			N	N	OW	N	N	N
<i>gularis</i>	P	Y	Y	I	R(>100)	OW	N	N	N
<i>virgatus</i>	P	N	N	N	N	OW	N	N	N
<i>nanus</i>	NM					OW	Y	Y	RRS
<i>erythrauchen</i>	NM					OW	Y	Y	RRS
<i>cirrhocephalus</i>	I			N	N	OW	N	N	N
<i>brachyurus</i>	NM					OW	Y	N	RRS
<i>rhodogaster</i>	NM					OW	Y	Y	CE
<i>madagascariensis</i>	NM					OW	N	Y	CE
<i>ovampensis</i>	P	N	N	N	N	OW	N	N	N
<i>nisus</i>	P	N	N	I	O(<10)	OW	N	N	N
<i>rufiventris</i>	I			N	N	OW	N	N	N
<i>striatus</i>	P	N	N	S	O(<10)	NW	N	N	N
<i>chionogaster</i>	NM					NW	Y	N	N
<i>ventralis</i>	NM					NW	Y	N	N
<i>erythronemius</i>	NM					NW	N	N	N
<i>cooperii</i>	P	N	N	S	O(<10)	NW	N	N	N
<i>gundlachi</i>	NM					NW	Y	Y	CE
<i>bicolor</i>	P	N	N	N	N	NW	N	N	N
<i>chilensis</i>	P	N	N	N	N	NW	N	N	N
<i>melanoleucus</i>	P	N	N	N	N	OW	N	N	N
<i>henstii</i>	NM					OW	Y	Y	CE
<i>gentilis</i>	P	N	N	S	N	C	N	N	N
<i>meyerianus</i>	NM					OW	Y	Y	N
<i>Buteo</i>									
<i>nitidus</i>	P	N	N	N	N	NW	N	N	N
<i>magnirostris</i>	I			N	N	NW	N	N	N
<i>lineatus</i>	P	N	N	S	O(<10)	NW	N	N	N
<i>ridgwayi</i>	NM					NW	Y	Y	RRS
<i>platypterus</i>	C	Y	Y	S	R(>1000)	NW	N	N	N
<i>leucorrhous</i>	I			N	N	NW	N	N	N
<i>brachyurus</i>	P	N	N	N	O(<10)	NW	N	N	N
<i>albigula</i>	P	N	N	N	N	NW	N	N	N
<i>swainsoni</i>	C	Y	Y	S	R(>1000)	NW	N	N	N
<i>albicaudatus</i>	P	N	N	N	O(<10)	NW	N	N	N
<i>galapagoensis</i>	NM					NW	Y	Y	RRS

Species	Type migrant ^a	Long-distance migrant ^b	Trans-equatorial migrant ^c	Water crossing behavior ^d	Flocking behavior ^e	World distribution ^f	Wholly tropical species ^g	Island-restricted species ^h	Endemic species ⁱ
<i>polyosoma</i>	P	N	N	N	N	NW	N	N	N
<i>poecilochrous</i>	I			N	N	NW	N	N	N
<i>albonotatus</i>	P	N	N	N	O(<10)	NW	N	N	N
<i>solitarius</i>	I			N	N	HI	Y	Y	RRS
<i>jamaicensis</i>	P	N	N	S	O(>10)	NW	N	N	N
<i>ventralis</i>	I			N	N	NW	N	N	N
<i>buteo</i>	P	Y	Y	S	R(>1000)	OW	N	N	N
<i>oreophilus</i>	P	N	N	N	N	OW	N	N	N
<i>brachypterus</i>	I			N	N	OW	N	Y	CE
<i>rufinus</i>	P	N	N	N	O(<10)	OW	N	N	N
<i>hemilasius</i>	P	N	N	N	N	OW	N	N	N
<i>regalis</i>	P	N	N	N	O(<10)	NW	N	N	N
<i>lagopus</i>	C	Y	N	I	R(>10)	C	N	N	N
<i>auguralis</i>	P	N	N	N	O(<10)	OW	Y	N	N
<i>augur</i>	I	N	N	N	1(<10)	OW	N	N	N
<i>archeri</i>	NM					OW	Y	N	RRS
<i>rufofuscus</i>	I			N	N	OW	N	N	N
<i>Falco</i>									
<i>naumanni</i>	C	Y	Y	L	R(>1000)	OW	N	N	N
<i>timunculus</i>	P	N	N	I	O(<100)	OW	N	N	N
<i>newtoni</i>	NM					OW	N	Y	CE
<i>punctatus</i>	NM					OW	Y	Y	RRS
<i>araea</i>	NM					OW	Y	Y	RRS
<i>moluccensis</i>	NM					OW	Y	Y	CE
<i>cechruides</i>	P	N	N	I	R(<10)	OW	N	N	N
<i>sparverius</i>	P	N	N	I	O(<10)	NW	N	N	N
<i>rupicoloides</i>	I			N	N	OW	N	N	N
<i>alopez</i>	P	N	N	N	N	OW	Y	N	N
<i>ardosiaceus</i>	P	N	N	N	N	OW	Y	N	N
<i>dickinsoni</i>	NM					OW	N	N	N
<i>zoniventris</i>	NM					OW	N	Y	CE
<i>chicquera</i>	P	N	N	N	N	OW	N	N	N
<i>vespertinus</i>	C	Y	Y	L	R(>1000)	OW	N	N	N
<i>amurensis</i>	C	Y	Y	L	R(>1000)	OW	N	N	N
<i>eleonorae</i>	C	Y	Y	L	R(>10)	OW	N	N	N
<i>concolor</i>	C	Y	Y	L	O(<10)	OW	N	N	N
<i>jemoralis</i>	P	N	N	S	N	NW	N	N	N
<i>columbarius</i>	P	Y	N	L	O(<10)	C	N	N	N
<i>rufifigularis</i>	I			N	N	NW	N	N	N
<i>deiroleucus</i>	I			N	N	NW	N	N	N
<i>subbuteo</i>	C	Y	Y	I	R(<100)	OW	N	N	N
<i>cuvierii</i>	I			N	O(<10)	OW	N	N	N
<i>severus</i>	P	N	N	S	O(<10)	OW	N	N	N
<i>longipennis</i>	P	N	N	I	N	OW	N	N	N
<i>novaezeelandiae</i>	P	N	N	I	N	OW	N	Y	CE
<i>berigora</i>	P	N	N	I	O(<10)	OW	N	N	N
<i>hypoleucos</i>	I			N	N	OW	N	N	CE
<i>subniger</i>	I			N	N	OW	N	N	CE
<i>biarmicus</i>	P	N	N	N	N	OW	N	N	N
<i>jugger</i>	I	N	N	N	N	OW	N	N	N
<i>cherrug</i>	P	Y	N	I	N	OW	N	N	N
<i>rusticolus</i>	P	N	N	L	N	C	N	N	N
<i>mexicanus</i>	P	N	N	N	N	NW	N	N	N
<i>pergrinus</i>	P	Y	Y	L	N	C	N	N	N
<i>fasciinucha</i>	NM					OW	N	N	N

^aNM = nonmigrants, C = complete migrants, P = partial migrants, and I = irruptive or irregular migrants (based on Zalles and Bildstein 2000).

^bComplete or partial migrants, 20% of whose populations (sometimes entire subspecies) regularly migrate more than 1,500 km.

^cComplete or partial long-distance migrants, at least 20% of whose populations (sometimes entire subspecies) regularly migrate across the equator.

^dN = none; S = short, <25 km; I = intermediate, 25–100 km; L = long, >100 km (Kerlinger 1989, with updates).

^eN = never or hardly ever; O = occasional, often with heterospecifics; R = regular, typically with conspecifics; (maximum flock size) (Kerlinger 1989, with updates).

^fOW = Old World species, NW = New World species (i.e., species found only in the Old World or New World, respectively), C = cosmopolitan species (i.e., species found in both the Old World and New World), HI = Hawaiian Islands.

^gSpecies distributed only in the Tropics.

^hSpecies found only on islands (including continental islands, oceanic islands, and archipelagos).

ⁱN = Not an endemic, CE = Country endemics (i.e., species restricted to a single country), RRS = Restricted-range species (i.e., species whose historic and current breeding ranges are larger than 50,000 km²) (based on Stattersfield et al. 1998).

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LITERATURE CITED

- Agostini, N., C. Coleiro, F. Corbi, G. Di Lieto, F. Pinos, and M. Panuccio. 2002. Water-crossing tendency of juvenile Honey Buzzards during migration. *Avocetta* 26:41–43.
- Agostini, N., and D. Logozzo. 1995. Autumn migration of Honey Buzzards in southern Italy. *Journal of Raptor Research* 29: 275–277.
- Alerstam, T. 1990. *Bird Migration*. Cambridge University Press, Cambridge.
- Ali, S., and S. D. Ripley. 1978. *Handbook of the Birds of India and Pakistan*, Vol. 1 (second ed.). Oxford University Press, Delhi and London.
- Bailey, R. G. 1989. Ecoregions of the continents: map and explanatory supplement. *Environmental Conservation* 16:307–309.
- Bednarz, J. C., and P. Kerlinger. 1989. Monitoring hawk populations by counting migrants. Pages 328–342 in *Proceedings of the Northeast Raptor Management Symposium and Workshop* (B. G. Pendleton, ed.). National Wildlife Federation, Washington, D.C.
- Belopolski, L. O. 1971. Migration of Sparrowhawk on the Courland Spit. *Notatki Ornithologiczne* 12:1–12.
- Berthold, P. 1999. A comprehensive theory of the evolution, control and adaptation of avian migration. *Ostrich* 70:1–11.
- Berthold, P. 2001. *Bird Migration: A General Survey* (second ed.). Oxford University Press, Oxford.
- Bildstein, K. L. 1999. Racing with the sun: the forced migration of the Broad-winged Hawk. Pages 79–102 in *Gatherings of Angels: Migrating Birds and their Ecology* (K. P. Able, ed.). Cornell University Press, Ithaca.
- Bildstein, K. L. 2004. Raptor migration in the Neotropics: patterns, processes, and consequences. *Ornitologia Neotropical* 15(Suppl.):83–99.
- Bildstein, K. L., and K. Meyer. 2000. Sharp-shinned Hawk (*Accipiter striatus*). *The Birds of North America*, no. 482 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia.
- Bildstein, K. L., W. Schelsky, J. Zalles, and S. Ellis. 1998. Conservation status of tropical raptors. *Journal of Raptor Research* 32:3–18.
- Bildstein, K. L., and J. I. Zalles. 2001. Raptor migration along the Mesoamerican Land Corridor. Pages 119–141 in *Hawk watching in the Americas* (K. L. Bildstein and D. Klem Jr., eds.). Hawk Migration Association of North America, North Wales, Penn.
- Blackburn, T. M., and R. P. Duncan. 2001. Determinants of establishment success in introduced birds. *Nature* 414:195–197.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography* (second ed.). Sinauer Associates, Sunderland, Mass.
- Brown, L., and D. Amadon. 1968. *Eagles, Hawks and Falcons of the World*. McGraw-Hill, New York.
- Cade, T. J. 1982. *The Falcons of the World*. Cornell University Press, Ithaca.
- Chong, M. 2000. Asian raptor migrations areas and population survey (Asian Raptor M. A. P. S.). *Asian Raptors* 1:12–15.
- Cox, C. B., and P. D. Moore. 2000. *Biogeography: An Ecological and Evolutionary Approach* (sixth ed.). Blackwell Science, Oxford.
- Darlington, P. J. 1957. *Zoogeography: The Geographical Distribution of Animals*. John Wiley and Sons, New York.
- del Hoyo, J. A. Elliot, and J. Sargatal. 1994. *Handbook of the Birds of the World*, Vol. 2. Lynx Ediciones, Barcelona.
- England, A. S., M. J. Bechard, and C. S. Houston. 1997. Swainson's Hawk (*Buteo swainsoni*). *The Birds of North America*, no. 265 (A. Poole and F. Gill, eds.). The Birds of North America, Inc. Philadelphia.
- Ferguson-Lees, J., and D. A. Christie. 2001. *Raptors of the World*. Houghton-Mifflin, Boston.
- Fleischer, R. C., and C. E. McIntosh. 2001. Molecular systematics and biogeography of Hawaiian avifauna. *Studies in Avian Biology* 22:51–60.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405:220–227.
- Geyr von Schweppenburg, H. F. 1963. Zur Terminologie und Theorie der Leitlinie. *Journal of Ornithology* 104:191–204.
- Glantz, M. H. 2001. Currents of Change: Impacts of El Niño and La Niña on Climate and Society. Cambridge University Press, Cambridge.
- Goodrich, L. J., S. C. Crocoll, and S. E. Senner. 1996. Broad-winged Hawk (*Buteo platypterus*). *The Birds of North America*, no. 218 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia.
- Grinnell, J. 1922. The role of the "accidental." *Auk* 39:373–380.
- Hagar, J. A. 1988. Migration (Broad-winged Hawk). Pages 12–25 in *Handbook of North American Birds*, Vol. 5 (R. S. Palmer, ed.). Yale University Press, New Haven.
- Hake, M., N. Kjellén, and T. Alerstam. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos* 103:385–396.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Kerlinger, P. 1989. *Flight Strategies of Migrating Hawks*. University of Chicago Press, Chicago.
- Krishnamurti, T. N. 1996. Monsoons. Pages 512–515 in *Encyclopedia of Climate and Weather* (S. H. Schneider, ed.). Oxford University Press, Oxford.
- Lam, C. Y., and M. Williams. 1994. Weather and bird migration in Hong Kong. *Hong Kong Bird Report* 1993:139–169.
- Mayr, E. 1943. The zoogeographic position of the Hawaiian Islands. *Condor* 45:45–48.

- Mayr, E., and J. Diamond. 2001. *The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography*. Oxford University Press, Oxford.
- McCanch, N. V. 1997. Sparrowhawk *Accipiter nisus* passage through the Gulf of Man. *Ringling & Migration* 18:1–13.
- Newton, I. 2003. *The speciation and biogeography of birds*. Academic Press, New York.
- Newton, I., and L. C. Dale. 1996. Bird migration at different latitudes in eastern North America. *Auk* 113:626–635.
- NOAA [National Oceanic and Atmospheric Administration]. 1988. *Constructed World-wide Tropical Cyclones 1871–1988*. Publication TD-9636. U.S. Department of Commerce, Washington, D.C.
- Pimm, S. L. 1991. *The Balance of Nature?* University of Chicago Press, Chicago.
- Primack, R. B. 2002. *Essentials of Conservation Biology* (third ed.). Sinauer Associates, Sunderland, Mass.
- Riesing, J. J., L. Kruckenhauser, A. Gamuf, and E. Haring. 2003. Molecular phylogeny of the genus *Buteo* (Aves: Accipitridae) based on mitochondrial marker sequences. *Molecular Phylogenetics and Evolution* 27:328–342.
- Rosenfield, R. N., and J. Bielefeldt. 1993. Cooper's Hawk (*Accipiter cooperii*). *The Birds of North America*, no. 75 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia.
- Rowlett, R. A. 1980. Migrant Broad-winged Hawks in Tobago. *Journal of the Hawk Migration Association of North America* 2:54.
- Schulter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- Shelley, E., and S. Benz. 1985. Observations of aerial hunting, food carrying and crop size of migrant raptors. Pages 299–301 in *Conservation Studies on Raptors* (I. Newton and R. D. Chancellor, eds.). International Council for Bird Preservation, Cambridge, U.K.
- Shirihai, H., R. Yosef, D. Alon, G. M. Kirwan, and R. Spaar. 2000. *Raptor Migration in Israel and the Middle East*. International Birding and Research Center, Eilat, Israel.
- Simpson, G. G. 1953. *The Major Features of Evolution*. Columbia University Press, New York.
- Snow, D. W. 1978. Relationships between European and African avifaunas. *Bird Study* 5:134–148.
- Spaar, R., and B. Bruderer. 1997. Optimal flight behavior in soaring migrants: a case study of migrating Steppe Buzzards *Buteo buteo vulpinus*. *Behavioral Ecology* 8:288–297.
- Stark, H., and F. Liechti. 1993. Do Levant Sparrowhawks *Accipiter brevipes* also migrate at night? *Ibis* 135:233–236.
- Stattersfield, A. J., M. J. Crosby, A. J. Long, and D. C. Wrege. 1998. *Endemic Bird Areas of the World*. BirdLife International, Cambridge, U.K.
- Thorup, K., T. Alerstam, M. Hake, and K. Kjellén. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society of London (Supplement) Biology Letter* 7:S1–S4.
- Viverette, C. B., S. Struve, L. J. Goodrich, and K. L. Bildstein. 1996. Decreases in migrating Sharp-shinned Hawks (*Accipiter striatus*) at traditional raptor-migration watch-sites in eastern North America. *Auk* 113:32–40.
- Wattell, J. 1973. *Geographical Distribution in the Genus Accipiter*. Nuttall Ornithological Club, Cambridge, Mass.
- Williamson, M. 1996. *Biological Invasions*. Chapman and Hall, London.
- Zalles, J. I., and K. L. Bildstein. 2000. *Raptor Watch: A Global Directory of Raptor Migration Sites*. BirdLife International, Cambridge, U.K., and Hawk Mountain Sanctuary, Kempton, Penn.

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Birds of Two Worlds

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