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THE GOLDEN EAGLE (*AQUILA CHRYSAETOS*) IN THE BALÉ MOUNTAINS, ETHIOPIA

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ABSRACT.—We studied Golden Eagles (*Aquila chrysaetos*) in the afro-alpine area (elevation 3500–4000 m) of the Balé Mountains in Ethiopia. We monitored seven territories from 1–5 successive years for a total of 26 territory-years. Home ranges varied from only 1.5–9 km^2, the smallest size recorded for the species. This was probably due to the abundance of prey, mainly hares and grass rats, that made up 50% and 30% of prey, respectively. Despite this, productivity of these Golden Eagles was quite low averaging only 0.28 young per occupied territory ($N = 25$). This was due to a large number of unmated territorial adults and poor breeding performance by pairs (0.4 young per pair per year, $N = 17$). The high density and frequent interspecific interactions with Verreaux's Eagles (*Aquila verreauxii*) were key factors affecting the dynamics of this Golden Eagle population. The unusual coexistence of these two closely related species was a novel component of the rich predator guild in the area that included five other wintering or resident eagle species. This richness was related to the high density of rodents and lagomorphs, a characteristic of the Ethiopian afro-alpine ecosystem.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *Verreaux's Eagle*; *afro-alpine habitats*; *Ethiopia*; *prey abundance*; *interspecific competition*; *productivity*.

El aguila dorada (*Aquila chrysaetos*) en las montanas Balé de Etiopía

RESUMEN.—Estudiamos el águila dorada (*Aquila chrysaetos*) en el área afro-alpina (elevacion 3500–4000 m) de las montañas Balé en Etiopía. Monitoreamos siete territorios de 1–5 años continuos para un total de 26 territorios/año. Los rangos de hogar variaron entre 1.5–9 km^2. Los mas pequeños reportados para la especie. Esto probablemente debido a la abundancia de presas, principalmente liebres y ratas de pastizales, las cuales representan el 50% y el 30% de las presas respectivamente. A pesar de esto la productividad de las águilas fue muy baja con un promedio de 0.28 juveniles por territorio ocupado ($N = 25$). Esto se debió al gran número de adultos territoriales sin pareja y al pobre desempeño reproductivo de las parejas (0.4 juveniles por pareja por año, $N = 17$). La alta densidad y las frecuentes interacciones intraespecíficas con las águilas Verreaux (*Aquila verreauxii*) fueron factores que afectaron la dinámica de esta población de águilas doradas. La inusual coexistencia de estas dos especies estrechamente relacionadas es un componente novedoso de la estructura de depredadores en el área que incluye otras cinco especies migratorias o residentes de águilas. Esta riqueza estuvo relacionada con la alta densidad de roedores y lagomorfos, una característica del ecosistema afro-alpino Etiope.

[Traducción de César Márquez]

The recent discovery of a Golden Eagle (*Aquila chrysaetos*) population in Ethiopia (Clouet and Barrau 1993) has provided a unique opportunity to study this species in a new biogeographical area. The population occurs in the Balé Mountains located in the southern part of the Ethiopian high plateau, east of the Rift Valley. It occurs at the afro-alpine region which supports the largest mountain moorland and grassland habitat on the continent. This rich and unique ecosystem (Dorst and Roux 1972, Hillman 1986) supports an avian community dominated by a predator-scavenger guild (Clouet et al. 1995). The Golden Eagle is part of a unique assemblage of eagle species and coexists with the

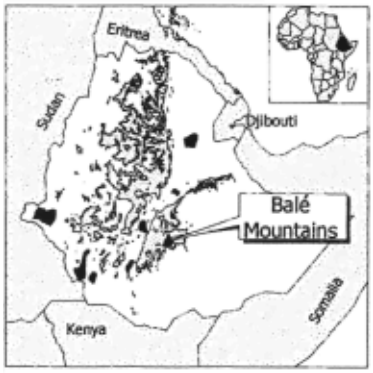

Figure 1. Location of the Balé Mountain study area in Ethiopia.

Verreaux's Eagle (*Aquila verreauxii*). To our knowledge, this assemblage that includes the southernmost extent of the Golden Eagle has never before been studied.

STUDY AREA AND METHODS

The study area was in Balé Mountains National Park in the upper Web River Valley and a portion of its tributaries above tree line (3500–4000 m) (Fig. 1). The area consists of a continuous network of cliffs stretching from the north bank of the Web River to the top of the Massif (Sanetti plateau). The afro-alpine habitat has a tropical climate tempered by the altitude and characterized by an alternating wet season that lasts from March–October and a dry season that lasts from November–February.

We searched for breeding raptors in a 200 km^2 area of potential nesting and hunting habitat over the course of seven expeditions covering five successive breeding seasons: August 1993, May 1994, March–November 1995, March 1996, and February–August 1997. One to three observers walked transects through Golden Eagle territories. Observations were made continuously for periods of 2–11 hr, recording the activities of the eagles and any interspecific behavior involving other raptors species. All eagle flights were plotted on a map to calculate their distances and areas covered. The total observation time for the seven expeditions was 210 h.

We estimated diet by observing kills and collecting prey items in nests during the fledging period. Diet diversity was calculated using a Shannon Index (Delibes et al. 1975, Clouet 1981, Fernández 1991). Productivity (number of young per occupied territory) was calculated by observing young in nests that were older than 51 d of age (Steenhof 1987) (except in one case when a nestling was only about 35-d old) or in flight with adults during the postfledging stage (August 1993, May 1994, and August 1997).

RESULTS

We identified seven territories occupied by Golden Eagles. We assumed that territories were centered on the occupied nest or, when the pair was not breeding or when it was occupied by an unpaired bird, we used the arithmetic center of the known unoccupied nests in the territory. The average distance between centers was 4.7 km (range = 2.5–7 km) (Fig. 2). Individual territories were monitored for 1–5 yr totaling 26 territory-years (Table 1). Single adults were observed in three out of the seven monitored territories and during 4 of the 5 yr of the study (i.e., seven (27%) of the 26 territory-years). Nonterritorial single birds were recorded only twice (1 adult and 1 immature eagle).

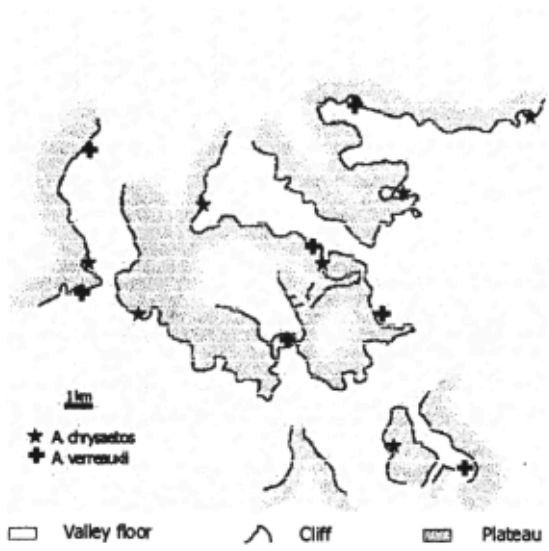

Figure 2. Distribution of Golden and Verreaux's Eagles in the 200-km^2 study area in the Balé Mountains National Park, Ethiopia, 1993–97.

Topographically, the territories included a section of cliff where perches and nests were located and a part of the neighboring plateau. The slope located at the foot of the cliff was comprised of scree, grassland, and bushes, and it provided a variety of potential prey including hyraxes (*Procavia capensis*), hares (*Lepus strarki*), and francolins (*Francolinus* spp.). In the valley bottom, there were also colonies of mole rats (*Tachyoryctes macrocephalus*) and grass rats (*Arvicanthis* spp. and *Lophuromys* spp.).

We observed nine successful kills by Golden Eagles. All were made either on low altitude flights by eagles close to the slopes at the foot of cliffs (once) or within 200–2000 m of perches (eight times). Golden Eagles were also seen robbing prey from an Augur Buzzard (*Buteo augur*), Pallid Har-

Table 1. Territory occupancy and productivity of Golden Eagles in the Balé Mountains National Park, 1993–97.

YEAR	TERRITORY			
	1	2	3	4
1993	Single adult	Adult pair	Single adult	—
(6–13 August)		1 young flying		
1994	Adult pair		Adult pair	Single adult
(5–17 May)		Adult pair		
1995	Single adult	1 young flying	Adult pair	Single adult
(21 March–5 April)		Adult pair		
1996	Single adult	Adult pair	Adult pair	Single adult
(4–15 March)				
1997	Adult pair	Adult pair	Adult pair	Adult pair
(3–12 February)			1 5-wk-old young	
(9–18 August)				

rier (*Circus macrourus*), Lanner Falcon (*Falco biarmicus*), and Steppe Eagle (*Aquila nipalensis*).

Undulating display flights and attacks on intruders of other raptor species were performed by both paired or unpaired Golden Eagles, both near and ≤1 km from perches, cliffs and nests. In the case of one unpaired territorial adult, undulating flights accounted for up to 51% of the total flying time (115 min) in November at the beginning of the breeding season suggesting that the function of this flight was to display its territory.

The mean area of the home ranges, estimated from observations of hunting forays and territorial flights, such as undulating displays and attacks on intruders, was 3.6 km^2 (range = 1.5–9 km^2, N = 7). Home ranges were smaller for single adults (1–1.5 km^2, N = 2) and appeared to be larger where there was no rodent colony or where scrub (*Erica* spp.) was extensive (estimated to be about 9 km^2).

Observations of kills (N = 9) and identification of prey items brought to nests (N = 41) showed a predominance of mammals which accounted for 86% of the prey: 25 hares (50%), 3 hyraxes (6%), 2 giant mole rats (4%), 13 grass rats (26%), 5 *Arvicanthis blicki* (10%), 1 *Lophuromys melanonyx* (2%), and 7 unidentified prey (14%). Small species were probably underestimated because they were often entirely consumed by eagles. Birds accounted for a smaller part of the diet (14%): 4 Moorland Francolins (*Francolinus psilolaemus,* 8%), 2 Blue-winged Geese (*Cyanochen cyanopterus,* 4%), and 1 unidentified bird. Mammals accounted for 90% of the total prey biomass and hares alone made up 78% of the biomass.

Other breeding raptors were observed in every Golden Eagle territory we observed, including one or two pairs of Augur Buzzards, one pair of Lanner Falcons and one pair of Common Kestrels (*F. tinnunculus*). Frequent mobbing behavior of these raptors triggered attacks by eagles. We observed Tawny Eagles (*A. rapax*) which were residents throughout the year and Greater Spotted Eagles (*A. clanga*), Lesser Spotted Eagles (*A. pomarina*), and Steppe Eagles which were either migrating through or spent the winter in the area flying over Golden Eagle hunting areas. The latter were very numerous and on several occasions approximately 30 were recorded simultaneously in flight in February. Steppe Eagles were observed attacking Golden Eagles on their prey (3 cases). Golden Eagles were also seen chasing off intruding Tawny and Steppe Eagles (3 cases).

The survey area contained seven territories of Verreaux's Eagles, all occupied by pairs. All pairs raised at least one young during the study period. The average distance between occupied nests was 5.2 km (range = 3–7 km). Observations at six territories showed that Verreaux's Eagles traveled from 12–13 km^2 on hunting forays and territorial flights and they established common boundaries between their territories. The mean distance between the nearest occupied nest or territory center of a Golden Eagle and a Verreaux's Eagle was 3.4 km (N = 12, range = 0.65–6.0 km). Territories of the two species were mutually exclusive. Interactions we recorded most often were attacks by Golden Eagles on Verreaux's Eagles (N = 21). Only one attack by a Verreaux's Eagle on a Golden Eagle was

Table 1. Continued.

TERRITORY		
5	6	7
—		
	—	—
Adult pair 1 10-wk-old young	—	—
Adult pair 1 7-wk-old young	—	—
Adult pair 1 7-wk-old young	Adult pair	—
Adult pair incubating 1 young flying with adults	Adult pair 1 9-wk-old young Adult pair	Adult pair

observed and it involved an attempted piracy at the boundary of two territories.

We recorded three types of behavior by the Golden Eagle toward Verreaux's Eagles ($N = 26$). One behavior we classified as tolerance. It occurred when one or a pair of Verreaux's Eagles flew at high altitudes (>500 m) ($N = 5$) above Golden Eagles. However, we observed birds of each species perched out of sight of each other on the same cliff at distances of <400 m. Flight and undulating display flight behaviors were triggered by a Verreaux's Eagle approaching within 500–1000 m of a Golden Eagle nest or perch ($N = 7$). Aggressive flight behavior toward an intruding Verreaux's Eagle occurred when the intruding eagle came within 500 m of an occupied nest or perch used by a Golden Eagle ($N = 14$). Aggressive flights usually ended when the intruder withdrew. In two cases, the interaction resulted in grappling of talons.

The most frequent and most intense interspecific encounters observed occurred when two Golden Eagle territories were located between two Verreaux's Eagle territories and where inter-nest distances were short. In this situation, the number of Golden Eagle flights per hour of observation (38 hr) was 1.74. Territory defense flights and undulating flights made up 32% and 24% of all flights ($N = 66$), respectively. When the species were farther apart ($N = 4$ territories), the number of flights per hour of observation (44 hr) was 1.98 and the number of undulating flights accounted for only 6% of the total number of flights observed ($N = 87$).

Golden Eagles began building nests in November and unsuccessful breeding pairs often continued building until February. We observed five nests containing a single eaglet between March and May and immatures were seen flying together with adults in May and August (Table 1). Judging from the age of the young we observed, we estimated that laying occurred from mid-November to mid-January, and that fledgling occurred from mid-March through the end of May. The beginning of the breeding season corresponded with the beginning of the dry season and the young left the nest at the beginning of the rainy season. This phenology corresponded to the breeding seasons of most other nesting raptors in the Balé Mountains. The nesting season for Verreaux's Eagles started a few weeks earlier than that of Golden Eagles and the first females began incubation in November. Young Verreaux's Eagles left their nests from March–June. Productivity of Golden Eagles was 0.42 young per territorial pair per year ($N = 19$, Table 2).

DISCUSSION

Our observations of Ethiopian Golden Eagles showed similarities with holarctic populations but

Table 2. Golden Eagle productivity in the Balé Mountains National Park and locations of neighboring Verreaux's Eagles.

TERRITORY	YEARS OF STUDY	PRODUCTIVITY (YOUNG/YEAR)	DISTANCE FROM NEIGHBORING VERREAUX'S EAGLE PAIR(S) (km)	LOCATIONS OF NEIGHBORING VERREAUX'S EAGLE PAIR(S)
2	5	0.40	2.7	different valley
3	4	0.25	0.65	same cliff
			3.0	same valley
5	3	1.0	1.2	different valley
			4.0	same valley

differed in terms of their use of space, population regulation, and the type of predator community into which they integrated. Even though our prey sample was limited, Ethiopian Golden Eagles appeared to select terrestrial prey of similar size to that taken by Golden Eagles in European and North American populations (Brown and Watson 1964, Murphy 1975, Delibes et al. 1975, Clouet and Goar 1980, Haller 1982, Steenhof and Kochert 1988, Fernández and Purroy 1990). The number of small-sized prey (<2 kg) such as grass rats, which was likely underestimated by our sampling method, showed that these Golden Eagles were opportunistic predators taking small prey items when they became available in sufficient quantities (Delibes et al. 1975, Fernández 1991, Watson et al. 1993). Because hares were predominant prey, diet diversity was low ($H' = 1.44$) in comparison with Golden Eagles in the Pyrénées ($H' = 2.77$) (Clouet 1981).

The density of Golden Eagles in the Balé Mountains matched the highest figures recorded in the western highlands of Scotland (one pair per 38 km^2, Watson et al. 1992) and in North America (one pair per 29–36 km^2, Phillips et al. 1990). The home range size we recorded was the smallest reported for the species.

In Europe, territory size can range from 40–160 km^2 (Clouet 1988). In the Swiss Alps, the home range of four breeding pairs ranged from 22–48 km^2, and core areas used for hunting that ranged from 6–16 km^2 (Haller 1982) were larger than the areas used in Ethiopia. Variation in density between different areas in Europe was associated with food availability (Tjernberg 1985, Watson et al. 1992). The home range size documented in North America was influenced by the amount of favorable prey habitat and became smaller where high quality prey habitat was abundant (Dixon 1937, Collopy and Edwards 1989, Marzluff et al. 1997). The abundance of prey and its availability throughout the year in the Balé Mountains was probably an important factor in explaining the high density and the small home ranges we observed. Both hares and rodents occurred in high numbers in the afro-alpine moorland and grassland of the Balé Mountains. Their abundance was estimated by Gottelli and Sillero-Zubiri (1990) during their study of the Ethiopian wolf (*Canis simiensis*). Hare density was 32 individuals/km^2 for a biomass of 120 kg/km^2. The biomass of mole and grass rats was estimated at 3000–4000 kg/km^2 (Gottelli and Sillero-Zubiri 1990). These values are more than 20 times the available biomass of rodents above the tree-line on the northern slopes of the Pyrénées where the size of Golden Eagle territories is roughly 20 times larger than in Ethiopia (Clouet 1991).

Prey abundance influences breeding performance both in Europe and in North America (Murphy 1975, Smith and Murphy 1979, Clouet 1981, Haller 1982, Thompson et al. 1982, Tjernberg 1983, Jenny 1992, Watson et al. 1992, Steenhof et al. 1997). Productivity of Golden Eagles ranging from 0.79–0.82 young per territorial pair per year have been reported in long-term studies in North America (Phillips et al. 1990, Bats and Moretti 1994, Steenhof et al. 1997). Productivity has been lower in most European studies ranging from 0.48–0.53 young per territorial pair per year in the Alps (Haller 1996) and Pyrénées (Clouet 1988). Watson (1997) found a significant negative correlation between breeding success and diet diversity. Where Golden Eagles had a narrow feeding niche they tended to breed more successfully than where the niche was broad. In Ethiopia, despite high prey abundance and low diet diversity, productivity was low. This was probably due to the fact that territorial pairs did not breed successfully every year and only raised a single eaglet per brood and, in some years, certain territories were occupied by only single adults (27% of the total 26 territory-years studied). The latter may have resulted from a lack of surplus birds in the population. Surplus birds have often been noted in Golden Eagle populations (Haller 1982, 1996, Marzluff et al. 1997) and can compose up to 30% of the population in the Alps (Clouet and Couloumy 1994). The lack of surplus birds in the Balé Mountains could have been due to human persecution, but we have no data to support this. It may also have been due to the absence of recruitment of individuals from outside the Balé Mountain range. Because the population is sedentary, there is little opportunity for interaction with populations located 2000 km further to the north (Thiollay and Duhautois 1976). No Golden Eagles have been observed on the banks of the Red Sea during migratory movements (Bruun 1985, Welch and Welch 1989). Finally, insufficient productivity could explain the absence of surplus birds. Our estimated 0.42 young fledged per territorial pair per year is very low for a Golden Eagle population. In other African eagle populations, breeding success is not related to food availability but is highly density de-

pendent (Thiollay and Meyer 1978, Gargett 1977, 1990, Simmons 1993). The effect of density has also been documented in Golden Eagle populations in Europe (Haller 1982, 1996, Jenny 1992). The reduced productivity (0.48 young per pair per year) recorded in the Swiss Alps has been interpreted as the consequence of a density-dependent regulation process. The major limiting factor in breeding success in the Alps is the frequency of interactions with unpaired nonterritorial surplus birds causing a negative feedback effect. Regular interactions with settled birds increases the proportion of nonbreeding pairs and depresses successful incubation (Haller 1982, 1996, Jenny 1992). Perhaps, in the Balé Mountains, interactions between Verreaux's and Golden Eagles have the same negative effect on reproduction as surplus Golden Eagles in the Alps. Productivity of Golden Eagle pairs appeared to be influenced by the proximity of neighboring Verreaux's Eagle pairs. For the closest nests (650 m apart on the same cliff), neither species succeeded in breeding simultaneously. Such interactions with other species of eagles are exceptional, making the situation in Ethiopia rather unique.

Golden Eagle coexistence with other eagle species such as with Bonelli's Eagles (*Hieraaetus fasciatus*) has been reported in the Mediterranean region. Apparently, the two species become ecologically isolated through their territoriality and diets (Brosset 1961, Cheylan 1977, Jordano 1981, Clouet and Goar 1984, Parellada et al. 1984, Fernández and Insausti 1986, Bahat 1989). In Israel, apparently competition between the two species results in a lower density of Golden Eagles in areas where Bonelli's Eagles are abundant and where both species maintain exclusive home ranges (Bahat 1989).

In Ethiopia, the Golden Eagle is integrated into the largest eagle assemblage known which includes five other *Aquila* species. Here, ecological isolation between Tawny Eagles (resident) and Steppe, Lesser, and Greater Spotted Eagles (winter only) develops through specialized use of habitat (less rocky than that of the Golden Eagle), temporal separation of breeding periods and partly through diet. The Verreaux's Eagle is morphologically and ecologically very similar to the Golden Eagle and it is generally regarded to be its African equivalent. Both species are of similar size, have a similar predation potential (Voous 1970, Brooke et al. 1972), feed on terrestrial prey, use similar nesting habitat and breed at the same time of the year. Evidently, the two species escape from interspecific competition by establishing mutually exclusive ranges and they use undulating display flights to advertise their territory boundaries (Harmata 1982, Collopy and Edwards 1989). The only niche parameter which actually distinguishes the two species is diet. Dietary studies in Africa show that Verreaux's Eagles prey almost exclusively on rock hyraxes which represent up to 98% of their food intake (Brown et al. 1982, Gargett 1990). The prey remains that we collected under Verreaux's Eagle nests confirmed that hyraxes also predominate in the diet of Verreaux's Eagles in the Balé Mountains. On the other hand, hyraxes represented only a very small part of the diet of Golden Eagles.

We believe that the unusual coexistence of Golden and Verreaux's Eagles is possible because the Ethiopian afro-alpine region supports a rich and dense rodent community (Yalden 1988) that makes possible the assemblage of the most diverse guild of raptors ever found at such a high altitude.

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