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TERRITORY SIZE, ACTIVITY BUDGET, AND ROLE OF UNDULATING FLIGHT IN NESTING GOLDEN EAGLES

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Abstract.—We quantified time and activity budgets and territory size of four pairs of nesting Golden Eagles (*Aquila chrysaetos*) in southwestern Idaho during 1977–1978 and 1978–1979. Eagle territory size averaged 3276 ha, ranging from 1161 to 4898 ha, and encompassed a variety of habitat types. Male and female eagles exhibited different daily activity patterns, reflecting differences in their parental care activities; males perched 77.9% and females 84.7% of the time. Flight activities comprised 22.1% and 15.4% of the male and female daily time budgets, respectively. Undulating flight was observed on 388 occasions, approximately 3.2 times per hour of flight among males and 2.2 times per hour of flight among females. Most of the observations occurred at or near territory boundaries and appeared to serve a territorial function.

TAMAÑO DEL TERRITORIO, PRESUPUESTO DE ACTIVIDADES Y EL ROL DEL VUELO ONDULATORIO DURANTE EL PERIODO REPRODUCTIVO DE *AQUILA CHRYSAETOS*

Resumen.—Durante 1977–1979 hicimos un presupuesto de las actividades y además cuantificamos el tamaño del territorio de 4 parejas de Águilas Doradas (*Aquila chrysaetos*) en un estudio que se llevó a cabo en el suroeste de Idaho. El tamaño del territorio varió de 1161 a 4898 ha ($\bar{x}$ = 3276 ha) y cubrió una gran diversidad de habitáculos. Ambos sexos exhiben durante el día diferentes patrones de actividades que se reflejan en diferencias en la conducta parental. Los machos pasan el 77.9% del tiempo posados mientras que las hembras el 84.7%. El vuelo comprende el 22.1% y 15.4% del tiempo utilizado por el macho y la hembra, respectivamente. Vuelo ondulatorio fue observado en 388 ocasiones, aproximadamente 3.2 veces por hora de vuelo entre los machos y 2.2 veces entre las hembras. La mayoría de estas observaciones fueron hechas en los bordes de los territorios o muy cerca a éstos, por lo que se cree que puedan tener una función territorial.

The nesting ecology of Golden Eagles (*Aquila chrysaetos*) has been studied extensively, with most work focusing on diet (Carnie 1954, Mollhagen et al. 1972, Olendorff 1976), food requirements (Brown and Watson 1964, Fevold and Craighead 1958, McGahan 1967), and productivity (Smith and Murphy 1973, Steenhoff and Kochert 1982). Behavior of adults and young at the nest site also is well documented (Collopy 1984, Ellis 1979); however, because logistical difficulties often thwart efforts to monitor adult eagle behavior away from the nest, our understanding of this aspect of eagle behavior is meager. We present data on the territory sizes and daily activity budgets of adult male and female Golden Eagles and discuss an unusual aspect of their behavior, undulating flight, that may function as a territorial display.

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STUDY AREA AND METHODS

Our study was conducted along the Snake River Canyon and surrounding upland desert plateau south of Boise, Idaho. This 195,063 ha area, known as the Snake River Birds of Prey Area, is administered by the Bureau of Land Management and lies within the Great Basin semi-desert shrub biome described by Whittaker (1975). The major vegetation types in the area include big sagebrush (*Artemisia tridentata*), grasses (*Poa* and *Bromus* spp.), black greasewood (*Sarcobatus vermiculatus*), and shadscale (*Atriplex confertifolia*). Approximately one-fifth of the Area is cultivated. A more detailed description of the vegetation can be found in U.S.D.I. (1979).

Behavioral data on adult eagles were collected during the chick-rearing period (hatching through fledging) at the same four nests in 1978 and 1979. Day-long observations at each study site were made once every 6 d from blinds 15–40 m away. Adults away from the nest were observed using binoculars and a 15–40× telescope from a truck positioned in a prominent location in the territory. Observation of one of the four adult male eagles used in this study was facilitated by monitoring the radio-transmitter that had been attached during a previous study (U.S.D.I. 1979). We recorded the amount of time each parent performed maintenance behavior (e.g., preening, stretching), perched on and off the nest, and used directional, soaring, or undulating flight. We could not determine the amount of time eagles actually hunted, because flying birds often were not hunting and perched birds occasionally attacked prey.

A total of 1248 daylight hours (86 observation days) were spent monitoring four Golden Eagle nesting sites in 1978 and 1979. Because the irregular topography made it difficult to directly observe the adult eagles throughout the day, our observations of males and females were restricted to 330 hr and 413 hr, respectively. We used these data to develop estimates of the territory sizes and time budgets.

Sex of the parent eagles was determined by size differences and behavior. We identified parents during each nest visit by using these characteristics and by comparing photographs taken during each visit. The sex of a parent away from the nest was confirmed when it visited the nest, when it was joined by its mate and their size difference compared, or when the location and sex of its mate was determined. For a detailed description of nest observation procedures see Collopy (1983a, 1984). To avoid biasing the time budget data, we did not record any behavioral information on the adult at the nest site until approximately one hour after entering the blind.

Throughout each observation period, data were collected on perch locations and flight paths of each of the eagles and recorded on aerial photographs and topographic maps. The boundary and size of the territories were quantified using the minimum area method (Mohr 1947). This method can overestimate the territory size of an animal if the boundaries are not well-defined; however, Golden Eagles in this population nest along the Snake River Canyon (U.S.D.I. 1979) and often have

contiguous territories. Furthermore, the outermost points at which we observed eagles perching or flying often were at places where territorial encounters with adjacent breeding pairs routinely occurred. Consequently, we believed this method provided a reasonable estimate of territory boundary and size.

The percent coverage of different habitat types within the territories of three of the four eagle pairs studied was determined by overlaying the established territory boundary (i.e., a convex polygon) on a digitized vegetation data base developed by the Bureau of Land Management for the Birds of Prey Area and calculating the areal coverage of habitat types found within that polygon (see Steenhof 1982 for details). A fourth territory was located outside the area covered by the computerized vegetation data base. The major habitat types within this territory were identified in the field and their boundaries plotted on 7.5 min U.S. Geologic Survey topographic maps. The percent coverage of these habitat types was measured using a planimeter.

RESULTS AND DISCUSSION

Territory size.—Territory sizes of the four nesting pairs of Golden Eagles studied during the 1978 and 1979 breeding seasons averaged 3276 ha, with individual territories averaging 1161, 2474, 4569, and 4898 ha in size. This variation in size probably can be attributed to habitat differences and resulting differences in prey densities.

Black-tailed jack rabbits are the most important food item in the diet of eagles on the Birds of Prey Area (Collopy 1983a, U.S.D.I. 1979). Using spot-light line transects Smith and Nydegger (1985) quantified black-tailed jack rabbit densities in the four major vegetation types in which they occurred on the Area during 1979–1982. Although yearly variation in abundance occurred, the relative numbers of jack rabbits in each of the habitats measured were fairly consistent. In 1979, the year in which our studies overlapped, jack rabbit densities were highest in greasewood habitats (1.454 per ha), followed by big sagebrush (0.786 per ha), shadscale saltbush/common winterfat (0.365 per ha), and big sagebrush/common winterfat (0.138 per ha) habitats.

A comparison of the habitat types found in the four territories suggested that territory size was inversely related to the amount of good jack rabbit habitat present (Table 1). Mudflat, the smallest of the territories we studied, was composed almost totally of black greasewood, the habitat in which jack rabbit densities were highest (Smith and Nydegger 1985). Although the topography surrounding the Mudflat site restricted our ability to observe eagles when they moved to the northwest corner of their territory, we considered the effect of this bias on our estimate of territory size relatively minor.

Con Shea, the second smallest eagle territory, had less greasewood than Mudflat but the most big sagebrush cover type of any of the four areas studied, another habitat in which jack rabbit densities were fairly high (Table 1). The second largest territory, Feedlot, was nearly twice the size

TABLE 1. Percent of major cover types and total area (ha) within four Golden Eagle nesting territories in southwestern Idaho, during 1978–1979. Cover type descriptions are provided in U.S.D.I. (1979).

Vegetation cover type	Nest site			
	Mudflat	Con Shea	Feedlot	Indian Cove
Big sage		25.6	3.2	5.1
Winterfat			2.6	
Shadscale	28.1	36.6	86.4	
Greasewood	70.2	10.2		
Saltbrush		12.7		
Native grasses		8.0		21.5
Crested wheatgrass				19.4
Agriculture	1.7	1.3	1.2	39.1
Riparian				3.1
River and misc.		5.6	6.6	11.8
Total area (ha)	1161	2474	4569	4898

of Con Shea. Most of this territory, however, was comprised of shadscale-dominated habitats which supported low jack rabbit densities. The pair of eagles nesting at the Indian Cove site had the largest territory studied; it was located on the Snake River and had, in addition to the riparian habitats, large areas of cultivated land and crested wheatgrass (*Agropyron desertorum*) seedlings within the territory. These cover types supported low jack rabbit densities (Smith and Nydegger 1985, U.S.D.I. 1979).

The mean territory size (3276 ha) found in this study is less than the average territory size reported for eagles in southern California (9324 ha; Dixon 1937), but is slightly larger than territory sizes reported for eagles in Utah (2300 ha; Smith and Murphy 1973). These differences may reflect differences in habitat types and prey densities, but certainly local topography, nesting densities, and sampling design influence these values.

Daily activity budget.—Males perched an average of 78% and females 85% of the daylight hours (Table 2). Males typically visited the nest site

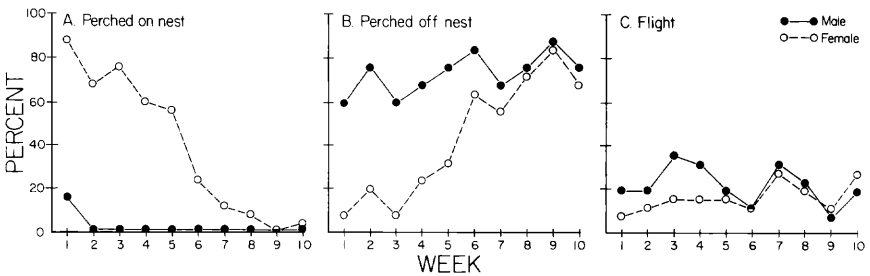

FIGURE 1. Percent of daylight hours that male and female Golden Eagles in southwestern Idaho perched on the nest, perched off the nest or were in flight. Data were combined from the four nest sites monitored during chick rearing in 1978 and 1979.

TABLE 2. Daily time and activity budgets (% of daylight hours) of four nesting pairs of Golden Eagles in southwestern Idaho during chick rearing in 1978 and 1979.

Activity	Males		Females	
	n (hrs)	%	*n* (hrs)	%
Perch				
On nest	4.2	1.3	147.3	35.6
Off nest	243.8	74.0	157.1	38.0
Self maintenance	4.5	1.4	3.2	0.8
Other	4.0	1.2	42.5	10.3
Subtotal	256.5	77.9	350.1	84.7
Flight				
Direct	6.4	1.9	3.6	0.9
Soaring	63.0	19.1	57.3	13.9
Undulating	1.2	0.4	0.4	0.1
Other	2.4	0.7	1.9	0.5
Subtotal	73.0	22.1	63.2	15.4
Total	329.5	100.0	413.3	100.1

only to deliver prey or nest materials; 74% of their time was spent perched at locations away from the nest. In contrast, females spent more time on the nest, perching, arranging nest material, and brooding or feeding young. As the chick-rearing period (hatching to fledging) progressed and as nestlings were better able to feed themselves and regulate their body temperature, females spent much less time on the nest (Fig. 1).

Male and female Golden Eagles flew an average of 22% and 15% of the time they were observed, respectively. The amount of time spent flying by each sex changed during the chick-rearing period (Fig. 1). Early in this period, females spent relatively little time flying, leaving the nest only for brief flights and feeding on prey delivered by the male. As chick rearing progressed, females spent less time at the nest, usually arriving only to deliver food and feed the young. Consequently, the amount of time they flew increased. Males provided most of the food throughout the nesting period (Collopy 1984) and, as a result, were often foraging away from the nest. After the fifth week of the nestling period, males and females were frequently together, even on hunting flights (see Collopy 1983b). This association resulted in the two sexes having similar activity budgets late in the chick-rearing period.

Overall, soaring was the most common type of flight used by males and females (Table 2). It was not possible, however, to assign any particular motivational state to soaring eagles, as they could have been traveling to a hunting site, hunting, performing displays, or flying without any obvious intent. Our observations suggested that each of these activities could occur while eagles soared. Directional flying accounted for a small fraction of the time budgets of male (1.9%) and female (0.9%) eagles. Other types of flight included agonistic interactions with Black-billed Magpies (*Pica pica*), Common Ravens (*Corvus corax*), American Kestrels

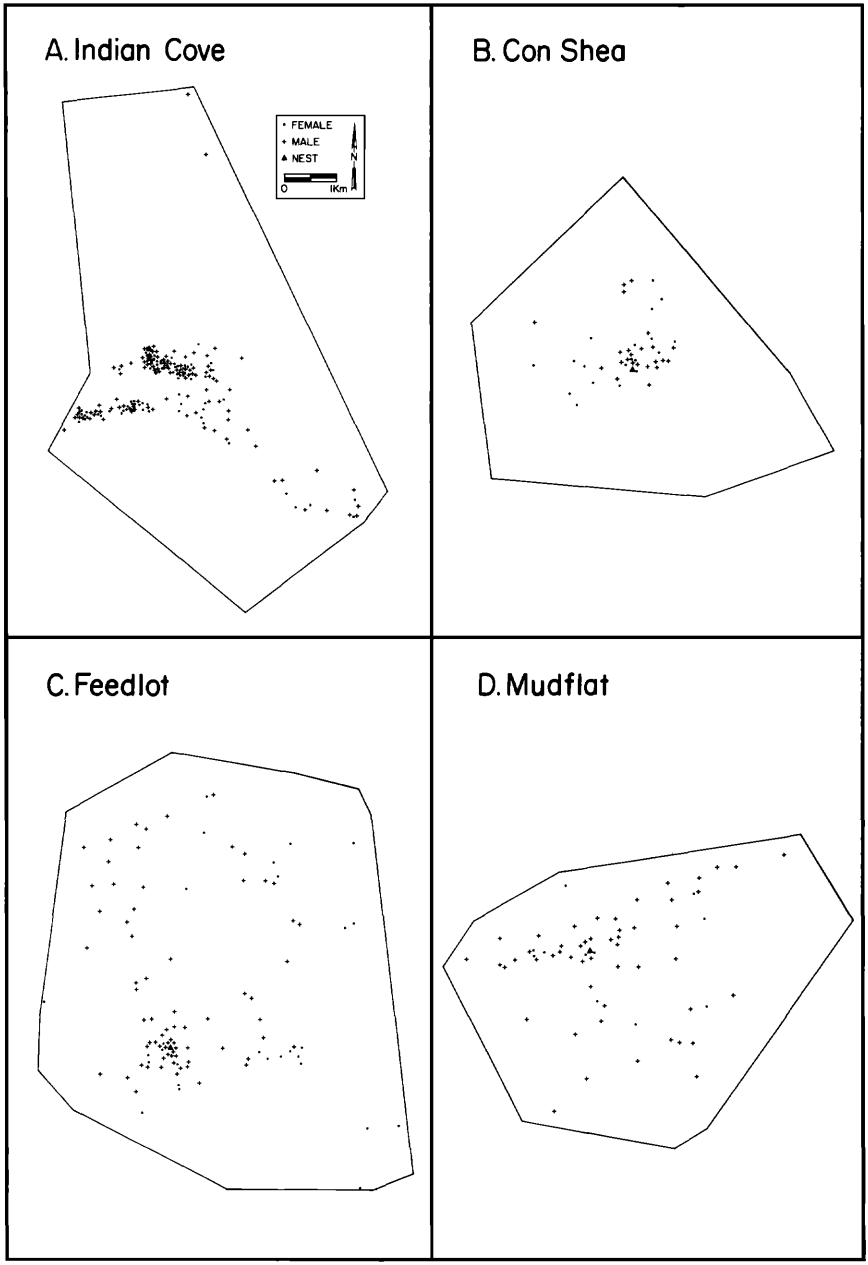

FIGURE 2. Location of undulating flight displays by male and female Golden Eagles within four territories studied in 1978 and 1979 in southwestern Idaho.

TABLE 3. Location and frequency of undulating flight displays by male and female Golden Eagles during 1978–1979 in southwestern Idaho. Only those undulating flights that were observed within approximately 400 m of the nest were considered to be associated with the nest site.

		Location of undulating flight			
		Nest site		Territory	
Site	Sex	*n*	%	*n*	%
Indian Cove	male	31	30.4	71	69.6
	female	23	29.1	56	70.9
Mudflat	male	14	27.5	37	72.5
	female	2	16.7	10	83.3
Con Shea	male	12	52.2	11	47.8
	female	5	26.3	14	73.7
Feedlot	male	24	33.3	48	66.7
	female	4	13.3	26	86.7
Totals	male	81	32.7	167	67.3
	female	34	24.3	106	75.7

(*Falco sparverius*), Prairie Falcons (*Falco mexicanus*), Northern Harriers (*Circus cyaneus*), and other Golden Eagles.

Undulating flight.—Undulating flight accounted for a very small portion of the time budget of male (0.4%) and female (0.1%) eagles (Table 2); however, its occurrence appeared to be an important feature of their behavioral repertoire. Undulating flight is initiated by a steep dive with wings folded, followed by an upward swoop with wings flapping at the apex of the climb (Brown and Amadon 1968, Harmata 1982). A total of 388 instances of undulating flight was observed during our study. On average, males performed 3.2 undulations per hour of flight, whereas females undulated 2.2 times during each hour of flight. This difference probably was due to the greater amount of time spent flying by the males early in the nesting season (see Fig. 2) when the incidence of territorial displays were highest.

Historically, undulating flight by Golden Eagles was thought to be a nuptial display that strengthened the pair bond (Bent 1937, Brown 1977, Brown and Amadon 1968). Recently, Harmata (1982) proposed that undulating flight by Golden Eagles was primarily a territorial and threat display stimulated by the presence of intruders. In support of this hypothesis, Harmata presented data on several aggressive responses by territorial eagles to intruders that contained undulating flight. He also documented that undulating flights occurred year-round and not just during the breeding season. In the Eurasian Sparrowhawk (*Accipiter nisus*), undulating displays over the nest site also are interpreted as a territorial display signalling that the site is occupied (Jones 1974, Newton 1986).

Our data support Harmata's (1982) interpretation that Golden Eagles perform undulating flight principally in a territorial context. During our study, most of the undulating flights by males (67.3%) and females (75.7%)

occurred away from the immediate vicinity of their mates or their nest (Table 3, Fig. 2). Moreover, these displays frequently occurred at the boundary of the territory or within view of an adjacent territorial eagle. On several occasions, for example, eagles from the Indian Cove site undulated simultaneously with adjacent territorial eagles at their respective boundaries to the west and southeast. Undulating displays also occurred over or in the immediate vicinity of the nest. It is not clear at this time if these flights are nuptial in nature or, as with Eurasian Sparrowhawks, signal the presence of a nesting pair.

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