

## Differential habitat selection by immature and adult Grey Eagle-buzzards *Geranoaetus melanoleucus*

JAVIER BUSTAMANTE<sup>1</sup>, JOSÉ ANTONIO DONÁZAR<sup>1</sup>, FERNANDO HIRALDO<sup>1</sup>,  
OLGA CEBALLOS<sup>2</sup> & ALEJANDRO TRAVAINI<sup>1</sup>

<sup>1</sup> Estación Biológica de Doñana, CSIC, Pabellón del Perú, Avda. María Luisa s/n, 41013 Sevilla, Spain

<sup>2</sup> Grupo de Estudios Biológicos Ugarrá, Carlos III 19, 31002 Pamplona, Spain

During the 1992 breeding season, we studied the habitat selection, behaviour, aggressive interactions and diet of immature and adult Grey Eagle-buzzards *Geranoaetus melanoleucus* in an area of the Argentinean Patagonia. Immature eagles selected areas rich in prey, had no preference for flat or rugged areas and did not avoid areas close to active nests or those used by adult eagles. The density of the European Hare *Lepus europaeus* was the best predictor of the distribution of immature eagles. Adult eagles preferred rugged to flat areas but were not significantly affected by prey distribution. Immature eagles used flapping flight more frequently than did adult eagles. Wing-flapping frequency of immatures did not differ when flying over slopes or plains. In contrast, adults used a more economic flight with a lower wing-flapping frequency than that of immatures, especially when flying over slopes. Adults, in contrast to immatures, tended to select slopes when flying over predominantly flat country. Only in 22% of the occasions when adult and immatures were seen together were immatures attacked by adults, a rate of aggressive encounters similar to that observed between immatures (32%). This similarity indicates that adults do not actively exclude immatures from certain areas. The main prey of both immature and adult eagles was the introduced European Hare followed by native rodents and birds. Immatures ate significantly more carrion and fewer birds than did adults. These observations suggest that differences in flight behaviour and in the flight silhouette between adult and immature eagles may be responsible for their different habitat selection in relation to topography. While immatures apparently cue on prey density for habitat selection, adults select areas that allow more economic foraging flights.

It is apparent, even to the casual observer, that raptors are habitat selective. Although other factors, notably nest site availability, are also influential, raptors are thought to select their habitat mostly in relation to its adequacy for foraging (Janes 1985). Most studies of habitat selection in raptors have focused on differential selection between species. But there have been studies showing intersex habitat differences in the American Kestrel *Falco sparverius* (Koplin 1973, Stinson *et al.* 1981, Bohall-Wood & Collopy 1986, Smallwood 1987), Marsh Harrier *Circus aeruginosus* and Hen Harrier *Circus cyaneus* (Schipper *et al.* 1975). Differences have also been reported between colour morphs of the Red-tailed Hawk *Buteo jamaicensis* (Preston 1980) and between age classes of the Bald Eagle *Haliaeetus leucocephalus* (Bennetts & McClelland 1991).

The theory of habitat selection (a branch of the theory of optimal foraging; Rosenzweig 1985) predicts that individuals will select the habitat in which they maximize their fitness. Within species, competition for resources can influence individual fitness, and according to the "despotic" mod-

el of habitat selection (Fretwell & Lucas 1969), dominant individuals through dominance and/or territorial behaviour prevent subordinates from exploiting certain habitats. In the dimorphic American Kestrel, the larger females select more open territories (which are of superior foraging quality) than do the males in their wintering areas in Florida (Smallwood 1987). In birds of prey in general, the more experienced adults holding breeding territories can exclude the less experienced immatures from habitats that are better for foraging.

Differences in colour, morphology or experience between individuals within one species can be related to habitat selection. Different colour morphs in the Red-tailed Hawk select different perching sites to obtain better concealment from prey (Preston 1980). Female Marsh Harriers, which are heavier and darker than males, prefer to hunt over higher and more structured vegetation to compensate for their more conspicuous colouration against the sky and their reduced agility (Schipper *et al.* 1975). Immature Bald Eagles prefer areas with higher availability of salmon carcasses,

while adults prefer areas with higher abundance of live salmon (Bennetts & McClelland 1991).

The Grey Eagle-buzzard *Geranoaetus melanoleucus* is a medium-sized diurnal raptor with a wide distribution in South America. Although it is conspicuous and relatively abundant, very little is known of its biology (Brown & Amadon 1968, Jiménez & Jaksic 1989, 1990).

Immature and adult Grey Eagle-buzzards differ in colouration and flight silhouette (Jiménez & Jaksic 1990). Immatures show a typical eagle silhouette with long straight wings and a long square tail. Adults have long pointed wings with long secondaries that form a continuum with the short rounded tail, giving the adult a characteristic triangular silhouette.

Our initial observations in the study area during the 1991 breeding season indicated that adults were more frequent on rugged landscapes while immatures were more frequent in flat, open areas. We considered three different models that could create a different spatial distribution of adult and immature Grey Eagle-buzzards in the study area.

(1) Adults nesting preferentially on cliffs and being necessarily central foragers during the breeding season may have limited access to flat areas far from their nest and would be found more frequently in rugged areas. Thus, during the breeding season, certain areas would be used less frequently by adults compared with immatures because the areas are far from active nests.

(2) Grey Eagle-buzzards may show a "despotic" distribution, with territorial adults excluding immatures from their breeding territories and immatures constrained to areas where no breeding pairs are found. Because most pairs select cliffs as nesting sites (Jiménez & Jaksic 1990, Travaini *et al.* 1994), flat, open areas far from cliffs would be the only areas available for immatures.

(3) Adult and immature Grey Eagle-buzzards may select different habitats because they select different prey that have a different distribution on the landscape or because they have different foraging strategies conditioned by their different silhouettes so that adults obtain some benefit by foraging over rugged landscapes or juveniles obtain some benefit by foraging over flat landscapes.

To test these models, we collected data on habitat selection of immature and adult Grey Eagle-buzzards in relation to distance from active nests, topography and prey abundance, on differences between adults and immatures in feeding habits and flight behaviour and also on prey distribution and abundance in the study area.

## STUDY AREA AND METHODS

The study was conducted in a rectangular area approximately 4400 km<sup>2</sup> (39°40'–40°20'S and 70°30'–71°15'W) centered at the city of Junín de los Andes, Neuquén province, northern Argentinean Patagonia. The landscape consisted of large plains at an altitude of 800–900 m, dissected by steep, rugged areas and valleys of different sizes. Altitude

ranged from 600 m to 2300 m and increased westward, toward the Andes. The area belongs to the Patagonian phytogeographic province, occidental district (Cabrera 1976). The vegetation was characterized by a mixed steppe of grass and shrubs. Dominant herbaceous plants were *Mullinum spinosum*, *Senecio* sp., *Stipa* sp. and *Poa* sp., while common shrubs were *Chacaya trinervis*, *Berberis darwinii* and *Schinus molle*. Trees were scarce; the commonest species were *Austrocedrus chilensis*, *Nothofagus* spp. and *Araucaria araucana*. The bottom of the valleys had humid areas with dense herbaceous vegetation, called "mallines", where dominant species were *Cortadeira araucana*, *Juncus* sp. and *Carex* sp. Trees like *Maytenus boaria* and the Willow *Salix humboldtiana* were concentrated in valleys and mallines.

The weather was dry and cold, with frosts almost throughout the year and frequent snowfalls in winter. Mean annual temperature was 11°C. The mean annual rainfall increased westward from 300 mm to 800 mm.

## Spatial distribution

Based on the models described above, we considered *a priori* three factors that could influence the distribution of immature and adult Grey Eagle-buzzards and subjectively selected two extreme levels for each factor: (1) proximity to active Grey Eagle-buzzard nests: close (less than 2 km from the nearest active nest, range 0.4–1.4 km) or far (more than 2 km from the nearest active nest, range 2.3–22 km), (2) topography: rugged (at least 75% of the area under observation was sloped) or flat (at least 75% of the area under observation was plains) and (3) prey abundance: rich or poor (we selected points in areas that we subjectively considered rich or poor in prey according to our previous knowledge of the area and a visual estimation of the abundance of herbaceous vegetation). Herbaceous vegetation abundance is correlated with the abundance of the European Hare *Lepus europaeus* (Novaro *et al.* 1992), the main prey of the eagle (Hiraldó *et al.* 1995). This approach produced eight possible combinations of factors. We selected 24 observation points on the study area, three different points for each of the eight combinations of factor levels (i.e. close-rugged-rich). Observation points had to be at least 2 km apart (range 2–11 km) and when they were replicates of the same combination of factors at least 6 km apart (range 6–33 km). An observation point was rejected and a new one selected if any of the four observers disagreed on the initial classification of the point according to topography or prey abundance.

At each observation point, counts were carried out on four different days, by a different single observer each time, to estimate the use of the area by immature and adult eagles. Two of the counts were carried out in the morning (09.00–14.00 h local time) and two in the afternoon (15.00–20.00 h). Each single point count lasted 3 h, making a total of 12 h of observation at each point. The observer looked in a predetermined fixed direction and recorded the number of "contacts" with immature or adult

Grey Eagle-buzzards (a contact being each time a single eagle was observed in, or entered, a 180° vision field in front of the observer). A 180° visual field was selected to exclude any active nest from the field of view at any point, to make observations predominantly over plains while still being close to a nest (most nests were on cliffs) and to maximize the amount of plains or slopes in the field of view at a specific point. Over homogeneous landscapes, with no constraints caused by nests, the 180° visual field was selected at random. Observers scanned the landscape in front of them with unaided eyes, using 10× binoculars only to identify the raptors once detected. Observers were initially assigned randomly to the observation points and rotated on consecutive days until the four counts at each point were completed. Observations were carried out between 25 November and 16 December 1992, and all except two of the 96 counts were carried out by the same four observers.

To assess our *a priori* estimates of prey abundance, two 1-h transects by foot, each performed by a different observer, were conducted at each point on two different evenings (19.00–21.00 h local time). Transects were conducted within the 180° field of view scanned by the observer in the area over which eagles were counted. All mammals and birds recorded by the observer were identified or classified into size categories.

To analyse the data on number of prey recorded during the transects and on the number of contacts with immature and adult Grey Eagle-buzzards, we used generalized linear models (GLM; Nelder & Wedderburn 1972, Dobson 1983, McCullagh & Nelder 1983) fitted with the program GLIM (Baker 1987). Because all the response variables were counts, we considered that errors would follow a Poisson distribution and used a log link (Crawley 1993). When the ratio deviance/degrees of freedom of the initial minimum adequate models suggested overdispersion in the data (probably because of a contagious distribution of the counts; Crawley 1993), the deviance of the model was scaled (a scale parameter being estimated from chi-square; Aitikin *et al.* 1989) and the significance of the final model was rechecked. This is the same as assuming that the variance of the error is equal to the mean multiplied by the scale parameter.

To check our *a priori* estimates of prey abundance and to confirm that prey abundance was independent of topography and proximity to a nest, we fitted a GLM model to the total number of individuals of four prey groups—European Hare, large birds (>1000 g), medium-sized birds (200–1000 g) and small birds (<200 g)—and pooled the counts of the two 1-h transects at each point. Initially, a maximal factorial model with *a priori* prey abundance, topography, distance to nest and the interaction between prey abundance and topography was fitted to the data. Each interaction or factor was eliminated from the model in turn. The interaction or factor that produced the smallest nonsignificant increase in deviance was eliminated, and the procedure was repeated until all the interactions or factors in the mod-

el produced a significant ( $P < 0.05$ ) increase in deviance when eliminated.

To test if the number of contacts with immatures or adults could be affected by the factors observer (six observers), wind speed (calm, moderate, strong), time of day (morning, afternoon) or the variable cloud cover (0–100%), we considered initially each 3-h point count as an independent observation. First, full models without interactions, but including the factors proximity to nest, topography and prey abundance, were fitted to the number of contacts with immatures and number of contacts with adults. The significance of observer, wind speed, time of day and cloud cover was assessed by stepwise backwards elimination from the full factorial model.

To check the significance of the effect of proximity to nest site, topography and prey abundance, the four 3-h counts at each point were pooled because the four counts are not independent observations. Full models with interactions between the factors proximity to nest, topography and prey abundance were then fitted to the data. As in the previous models, the significance of interactions and main effects was assessed by stepwise backwards elimination from the full factorial model.

Finally, we tested if the factorial models for immature and adult Grey Eagle-buzzard counts could be improved by using as predictors the number of prey counted at the transects or by using the number of adult or immature eagles counted at the point. The significance of each variable was assessed by the decrease of the scaled deviance of the model when the variable was included in the minimum adequate factorial model, following a standard forward stepwise procedure. The most significant variable was included in the model, and the process was repeated. When a new variable was included, we also checked if factors previously in the model remained significant, and if not, they were excluded.

### Flight behaviour

Every time a contact with a Grey Eagle-buzzard was made, the observer recorded (1) the type of flight classified into one of four categories: flapping, soaring, gliding or hovering (defined as a stationary flight wherein the eagle faced into a wind updraft and controlled its position with wing and tail movements [Jiménez & Jaksić 1989]), (2) the altitude of the flying bird and (3) the type of landscape over which the bird was flying. If the individual changed its flying behaviour during the observation, only the flying behaviour when first observed was recorded. If a bird was observed long enough, the observer timed with a stopwatch the number of wing flaps in a period of 30–120 s and estimated the rate of wing flaps per minute for that flight. The distributions of contacts with immature and adult Grey Eagle-buzzards in different flight types and over different types of landscapes were compared by Fisher's exact test and chi-square tests with Yates' correction for continuity where appropriate (Siegel & Castellan 1988). When applicable, the chi-square tables were partitioned in independent  $2 \times 2$

**Table 1.** Analysis of deviance table for a GLM model of the number of contacts with immature Grey Eagle-buzzards on each 3-h count, using Poisson errors and a log link. Significance assessed by stepwise omission of nonsignificant terms beginning from the maximal model. Models scaled because of significant overdispersion

Explanatory variable	Increase in scaled deviance	d.f.	Mean scaled deviance	F-ratio	P
Prey abundance <sup>a</sup>	16.2	1.94	16.2	19.4	<0.01
Proximity to nest	2.7	1.93	2.7	3.3	n.s.
Topography	0.6	1.92	0.6	0.7	n.s.
Observer	7.4	5.87	1.5	1.9	n.s.
Wind speed	1.2	2.85	0.6	0.8	n.s.
Time of day	0.6	1.84	0.6	0.8	n.s.
Cloud cover	0.6	1.83	0.6	0.7	n.s.

Note: Scaled deviance of maximal model = 65.21, d.f. = 83. Scale parameter = 4.25.

<sup>a</sup> Variable included in the minimum adequate model.

subtables to detect where the differences were (Siegel & Castellan 1988). Differences between immatures and adults in median flying altitude and median wing-flapping rate were tested with Wilcoxon-Mann-Whitney tests (Siegel & Castellan 1988). To test for an interaction in the wing-flapping rate between age of the eagle and topography of the landscape over which it was flying, we carried out an ANOVA with procedure GLM of SAS Institute Inc. (1987), using type III sum of squares on the square root of the wing-flapping rate of individual flights.

### Aggressive interactions

We recorded the number of instances when two or more Grey Eagle-buzzards were observed simultaneously and whether or not any interactions took place.

**Table 2.** Analysis of deviance table for a GLM model of the number of contacts with adult Grey Eagle-buzzards on each 3-h count, using Poisson errors and a log link. Significance assessed by stepwise omission of nonsignificant terms beginning from the maximal model. Models scaled because of significant overdispersion

Explanatory variable	Increase in scaled deviance	d.f.	Mean scaled deviance	F-ratio	P
Proximity to nest <sup>a</sup>	25.6	1.93	25.6	32.6	<0.01
Topography <sup>a</sup>	14.1	1.93	14.1	17.9	<0.01
Time of day	2.8	1.92	2.8	3.6	n.s.
Prey abundance	2.5	1.91	2.5	3.4	n.s.
Observer	2.6	5.86	0.5	0.7	n.s.
Wind speed	0.7	2.84	0.4	0.5	n.s.
Cloud cover	0.2	1.83	0.2	0.3	n.s.

Note: Scaled deviance of maximal model = 64.31, d.f. = 83. Scale parameter = 2.59.

<sup>a</sup> Variable included in the minimum adequate model.

### Feeding habits

During the breeding seasons of 1991 and 1992, the diet of adult Grey Eagle-buzzards was studied by Hiraldo *et al.* (1995), based on pellets found at the nests and at nearby perches. Data on prey of immature Grey Eagle-buzzards came from pellets collected at a communal roost used only by immatures. Pellets were collected in November 1991 (43 pellets), October and November 1992 (78 pellets) and May 1993 (eight pellets). Pellets were dried, and their contents were identified using a reference collection (birds, small mammals) and a key to small mammal skulls (O.P. Pearson, unpubl.). Mammal hairs were identified through medulla types and scale patterns following the methodology of Brunner and Coman (1974) and the keys of Chehébar and Martin (1989). Each prey species found in a pellet was considered one prey item unless there was clear evidence of more than one prey. Diets of immature and adult eagles were compared with chi-square tests. This information was supplemented with observations on the numbers of immature and adult eagles attracted to 37 sheep and hare carcasses. Throughout the text, means  $\pm$  s.d. are provided.

## RESULTS

### Prey distribution

For the main prey of the eagle, the transects provided information on the density of European Hares and birds but no information on rodents. Other medium-sized mammals like the "Pichi" *Zaedyuus pichiy* and the Hog-nosed Skunk *Conepatus chinga* were occasionally seen on the transects, but their numbers were too low to consider them in the analyses. Prey density data are given throughout as mean number of individuals seen in two transects.

The areas considered by us *a priori* as rich had significantly more prey than areas considered *a priori* as poor (European Hare,  $5.1 \pm 3.4$  v  $0.8 \pm 1.5$ ,  $F_{1,22} = 17.4$ ,  $P < 0.01$ ; large birds,  $13.3 \pm 77.2$  v  $4.0 \pm 5.3$ ,  $F_{1,21} = 6.8$ ,  $P$

**Table 3.** Analysis of deviance table for a GLM model of the number of contacts with immature Grey Eagle-buzzards at each observation point (the four 3-h counts pooled), using Poisson errors and a log link. Significance assessed by stepwise omission of nonsignificant terms beginning from the maximal model. Models scaled because of significant overdispersion

Explanatory variable	Increase in scaled deviance	d.f.	Mean scaled deviance	F-ratio	P
Prey abundance (P) <sup>a</sup>	8.9	1.22	8.9	7.8	<0.05
Proximity to nest (N)	1.5	1.21	1.5	1.3	n.s.
Topography (T)	0.3	1.20	0.3	0.3	n.s.
Interaction P × N	1.5	1.19	1.5	1.3	n.s.
Interaction T × N	0.1	1.18	0.1	0.1	n.s.
Interaction T × P	0.0	1.17	0.0	0.0	n.s.
Interaction T × N × P	0.1	1.16	0.1	0.0	n.s.

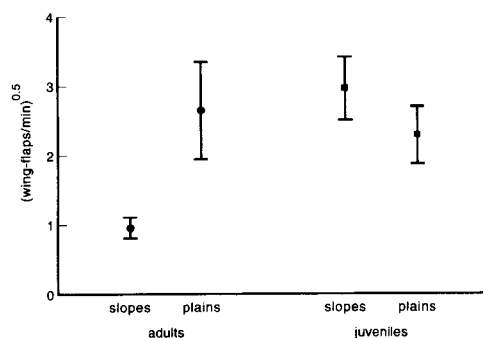
Note: Scaled deviance of maximal model = 21.51, d.f. = 16. Scale parameter = 7.72.

<sup>a</sup> Variable included in the minimum adequate model.

< 0.05; medium-sized birds,  $71.9 \pm 73.2$  v  $10.4 \pm 16.6$ ,  $F_{1,21} = 21.7$ ,  $P < 0.01$ ; small birds,  $12.1 \pm 9.6$  v  $3.6 \pm 4.3$ ,  $F_{1,21} = 10.0$ ,  $P < 0.01$ ). None of the differences in the numbers of European Hare could be attributed to topography ( $F_{1,21} = 0.02$ ), proximity to a Grey Eagle-buzzard nest ( $F_{1,20} = 0.02$ ) or the interaction between the *a priori* prey abundance and topography ( $F_{1,19} = 1.12$ ). Large and medium-sized birds were significantly more abundant in flat than in rugged areas ( $F_{1,21} = 7.9$ ,  $P < 0.05$ , and  $F_{1,21} = 12.5$ ,  $P < 0.01$ , respectively), but no differences could be attributed to the proximity to a nest site or to the interaction of topography and *a priori* prey abundance. The abundance of small birds showed a significant interaction between the prey abundance and topography ( $F_{1,20} = 4.53$ ,  $P < 0.05$ ) because rich and poor rugged areas had relatively similar counts of small birds in the transects ( $9.3 \pm 5.2$  v  $5.7 \pm 5.4$ ), which were intermediate between those in flat rich ( $14.8 \pm 12.6$ ) and flat poor areas ( $1.5 \pm 0.6$ ).

### Distribution of immature and adult eagles

There were no significant differences in the number of contacts with immature and adult Grey Eagle-buzzards related



**Figure 1.** Wing-flapping frequency, square root transformed (mean  $\pm$  s.e.), of adult (circles) and immature (squares) grey Eagle-buzzards flying over slopes or plains.

to observer, time of day, wind speed or percentage of cloud cover during the census (Tables 1 and 2).

The initial minimum adequate factorial model for the number of contacts with immature Grey Eagle-buzzards at each point indicated that immature eagles were significantly more frequent in areas considered to be rich in prey ( $9.2 \pm 12.2$ ) than in areas poor in prey ( $1.7 \pm 2.4$ ) and that there was no effect of proximity to an active nest or topography and no significant interaction between the factors (Table 3).

We tested if this factorial model could be improved using the prey counts gathered from the two 1-h transects. Two variables significantly improved the model: European Hare ( $F_{1,21} = 7.27$ ,  $P < 0.05$ ) and large birds ( $F_{1,21} = 5.97$ ,  $P < 0.05$ ). When the numbers of European Hare were included in the model, our prey abundance factor was no longer significant ( $F_{1,21} = 0.61$ ). The new minimum adequate model indicated that the number of contacts with immature Grey Eagle-buzzards had a positive correlation with the number of European Hares but a negative correlation with the number of large birds (Table 4). Neither topography, distance to an active nest nor number of contacts with adults significantly improved the model ( $F_{1,20} = 0.25$ ,  $F_{1,20} = 0.65$ ,  $F_{1,20} = 0.60$ , respectively). Inspection of the residuals of the model showed an outlier (a point with a count of 273 large birds) with a high potential influence in the model (small residual). We fitted a new model without this observation,

**Table 4.** Minimum adequate GLM model, using Poisson error and a log link, for the number of contacts with immature Grey Eagle-buzzards. The equation of the model is  $\text{Ln } Y = a + b_1X_1 + b_2X_2$

	Estimate	s.e.
Constant (a)	0.6588	0.4056
European Hare	0.2847	0.0562
Large birds	-0.0404	0.0203

Note: Scale deviance = 21.27, d.f. = 21. Scale parameter = 4.89.

**Table 5.** Analysis of deviance table for a GLM model of the number of contacts with adult Grey Eagle-buzzards at each observation point (the four 3-h counts pooled), using Poisson errors and a log link. Significance assessed by stepwise omission of nonsignificant terms beginning from the maximal model. Models scaled because of significant overdispersion

Explanatory variable	Increase in scaled deviance	d.f.	Mean scaled deviance	F-ratio	P
Proximity to nest (N) <sup>a</sup>	19.6	1,21	19.6	14.8	<0.01
Topography (T) <sup>a</sup>	10.8	1,21	10.8	8.1	<0.01
Prey abundance (P)	1.9	1,20	1.9	1.5	n.s.
Interaction P × N	1.8	1,19	1.8	1.4	n.s.
Interaction T × N	1.1	1,18	1.1	0.9	n.s.
Interaction T × P	0.4	1,17	0.4	0.3	n.s.
Interaction T × N × P	0.2	1,16	0.2	0.1	n.s.

Note: Scaled deviance of maximal model = 22.32, d.f. = 16. Scale parameter = 5.56.

<sup>a</sup> Variable included in the minimum adequate model.

and both variables, European Hares and large birds, remained significant ( $F_{1,20} = 26.08$ ,  $P < 0.01$  and  $F_{1,20} = 6.05$ ,  $P < 0.05$ , respectively), while the estimates for the parameters of the model remained almost the same.

The minimum model for number of contacts with adult Grey Eagle-buzzards indicated that contacts (given as mean number of contacts in 12 h) were significantly more frequent close to a nest site ( $15.3 \pm 15.1$ ) than far from it ( $3.0 \pm 3.1$ ), but they were also significantly more frequent on rugged areas ( $13.8 \pm 15.9$ ) than on flat areas ( $4.5 \pm 4.5$ ). The *a priori* prey abundance had no significant effect, and there was no significant interaction between the factors (Table 5).

We tried to improve this model by including the variables related to prey abundance, but none of them significantly improved the model (European Hare:  $F_{1,20} = 1.18$ , large birds:  $F_{1,20} = 0.29$ , medium-sized birds:  $F_{1,20} = 0.08$ , small birds:  $F_{1,20} = 1.01$ ), nor could it be improved by including the abundance of immature Grey Eagle-buzzards as predictor ( $F_{1,20} = 0.26$ ). The final minimum adequate model is presented in Table 6.

### Aggressive interactions

Out of 298 contacts with Grey Eagle-buzzards, 77% were contacts with one eagle, 20% with two eagles and 3% with

**Table 6.** Minimum adequate GLM model, using Poisson error and a log link, for the number of contacts with adult Grey Eagle-buzzards. The equation of the model is  $\ln Y = a + b_1X_1 + b_2X_2$

	Estimate	s.e.
Constant (a)	3.14	0.196
Proximity to a nest site (far)	-1.63	0.429
Topography (flat)	-1.12	0.369

Note: Scale deviance = 27.73, d.f. = 21. Scale parameter = 5.56.

groups of three eagles. No cases of aggression were observed in 30 contacts with pairs of adults and one contact with a group of three adults. Aggressive interactions were observed in four out of 18 contacts (22%) with mixed groups of adults and immatures (two or three individuals) flying together. In all four instances, one adult flew toward or chased away one immature. All aggressive interactions observed took place at points close to a nest. Aggressive interactions were observed in six instances out of 19 contacts (32%) with groups of immatures (two or three individuals).

### Flight behaviour, selection of topography

The general topography of the observation point, rugged or flat, influenced the type of landscape over which contacts with flying adult and immature eagles were made. At points classified as rugged, 96% of contacts with flying eagles were over slopes, and on points classified as flat, 79% of contacts were over plains. When observation points in rugged and flat areas were analysed separately, on rugged areas there was no difference in the distribution of contacts of immature and adults over slopes or plains (Fisher's exact test, n.s.), but on flat areas adults were observed proportionally more frequently flying over slopes (37% of contacts) than were immatures (4%; Fisher's exact test,  $P < 0.0001$ ; Table 7).

**Table 7.** Number of contacts with immature and adult Grey Eagle-buzzards flying over slopes or plains at observation points in rugged landscapes (more than 75% of the landscape covered by slopes) and in flat landscapes (more than 75% of the landscape covered by plains)

	Rugged landscapes		Flat landscapes	
	Slopes	Plains	Slopes	Plains
Adults	158	7	19	32
Immatures	69	1	2	48

**Table 8.** Number of contacts with adult and immature Grey Eagle-buzzards classified according to flight type they were using when first seen

Flight type	Adults	Immatures	Summary of partitioned chi-square	
			Partition	$\chi^2$
Gliding	104	43		
Soaring	61	32	1	0.66
Hovering	24	6	2	1.48
Flapping	27	36	3	16.51*
Total	216	117	Overall	18.65*

\*  $P < 0.001$ .

### Types of flights used by adults and immatures

The proportions of flight types used by immatures and adults (classified as flapping, gliding, soaring and hovering) differed significantly ( $\chi^2_3 = 18.7$ ,  $P < 0.001$ ). If the degrees of freedom of the  $4 \times 2$  contingency table are partitioned (Siegel & Castellan 1988), there were proportionally more contacts with immatures in flapping flight than with adults ( $\chi^2_1 = 16.5$ ,  $P < 0.001$ ), but the differences in the number of contacts between gliding, soaring and hovering flights were not significant (Table 8).

### Wing-flapping frequency

In 101 contacts with adults and in 54 with immatures, it was possible to measure the wing-flapping frequency. Adults had a median wing-flapping frequency of 1 wing-flap per min (range 0–80), and immatures had a median wing-flapping frequency of 5 wing-flaps per min (range 0–55). The difference in wing-flapping frequency between adults and immatures was highly significant (two-tailed Wilcoxon-Mann-Whitney test,  $z = 4.12$ ,  $P < 0.0001$ ). When wing-flapping frequency was analysed in relation to age and topography, a very significant interaction was found ( $F_{1,147} = 9.75$ ,  $P < 0.002$ ). Immatures showed a relatively high wing-flapping frequency when flying over both slopes and plains, while adults showed low wing-flapping frequency when flying over slopes but the same wing-flapping frequency as immatures when flying over plains (Fig. 1).

### Flight altitude

In 211 contacts with adults and 112 contacts with immatures, the observers estimated the altitude at which the individual was flying when first seen. Flying altitudes ranged from 1 m to over 100 m. The median flying altitudes were 35 m for adults and 40 m for immatures. There were no significant differences in flying altitude between adults and immatures (two-tailed Wilcoxon-Mann-Whitney test,  $z = 1.21$ , n.s.).

**Table 9.** Percentage of occurrence of prey categories in the diets of immature and adult Grey Eagle-buzzards in Neuquén province, Argentina. Data on the diet of adults from Hiraldo *et al.* (1995)

Prey type	% of immature diet	% of adult diet
<b>Mammals</b>		
Unidentified mammals or carrion	6	3
European Hare	59	58
Other medium-sized mammals	2	1
Rodents	17	19
Total mammals	83	81
<b>Birds</b>		
Large birds (>1000 g)	1	1
Medium-sized birds (200–1000 g)	5	5
Small birds (<200 g)	2	5
Unidentified birds	2	7
Total birds	9	16
Reptiles	3	2
Fish	0	<1
Invertebrates	4	1
No. of prey	187	1254

### Feeding habits

The examination of 187 prey items from immature Grey Eagle-buzzards revealed that they fed mainly on European Hares (59%), followed by rodents (17%) and birds (9%; Table 9). The diet of the immature eagles, considering six prey groups (mammal carrion + unidentified mammals, European Hare, medium-sized mammals, rodents, birds and other prey), was significantly different ( $\chi^2_5 = 24.1$ ,  $P < 0.001$ ) from that of the breeding adults studied in the same area by Hiraldo *et al.* (1995). Partitioning the degrees of freedom of the chi-square table revealed that adults and immature eagles did not differ in the proportions of European Hare, medium-sized mammals and rodents in their diets, but immature eagles exploited carrion ( $\chi^2_1 = 3.9$ ,  $P < 0.05$ ) and other prey ( $\chi^2_1 = 10.9$ ,  $P < 0.001$ ) significantly more often than did adults, and adults preyed significantly more frequently on birds than did immatures ( $\chi^2_1 = 5.4$ ,  $P < 0.02$ ). Also, 88 out of 94 eagles that were attracted to and fed on carcasses put out by us were immatures. The proportion differed significantly from the relative proportion of immatures in the population, as estimated from the number of contacts with immatures at observation points far from active nests (46 out of 82 contacts with eagles, binomial test,  $z = 7.74$ ,  $P < 0.01$ ).

### DISCUSSION

It is clear from our results that immature Grey Eagle-buzzards distribute themselves in the study area according to

the density of their main prey, the European Hare. The negative relation found between immature eagle distribution and density of large birds, consisting of Buff-necked Ibis *Theristicus caudatus* and geese *Chloephaga* spp., might be because of a certain avoidance by the eagle of the flooded mallines where these species were most abundant, even though hares were also relatively abundant in them. Large birds had a relatively low occurrence in the diet of the eagle (Table 9), and it is possible they all were consumed as carrion. The tall, dense vegetation of the flooded mallines might make them less attractive to immature eagles because of the difficulty of detecting prey (Janes 1985).

In contrast, adult eagles did not seem to be affected in their distribution by prey density. Neither our initial estimates of prey abundance nor the counts of hares or birds were good predictors of the use of a certain area by adult eagles. Adult eagles were more frequent close to their nests as expected because of the constraint of being central foragers during the nesting season, but they also selected rugged areas over flat areas. When flying over predominantly flat areas, adults, in contrast to immatures, selected the slopes. Also, there were no differences in prey counts related to proximity to a nest, suggesting that prey abundance was not an important factor in nest-site selection by the eagles in the area.

We can reject the first of our initial hypotheses, that adults are constrained to rugged areas because of the distribution of adequate nesting places, because our data show that adults preferred rugged areas over flat areas even when the factor proximity to the nest was taken into account. The second hypothesis, that adult and immature eagles showed a "despotic" distribution and that immatures were excluded by adults from the best areas, can also be rejected. Immatures were not affected in their distribution either by proximity to an active nest or by the presence of adult eagles. Neither the adults nor the nests were found in the areas of higher prey abundance. Finally, although adults showed dominance over immatures in aggressive interactions, these were not more frequent than aggressive interactions among nonterritorial immatures, and even then, in most instances the immatures were not chased away from the area by the adults.

The third hypothesis, that adult and immature eagles select different habitats, is the only one not rejected by our data. Adult and immature eagles could have been selecting different habitats because they fed on different prey that had a different distribution on the landscape. Although there were significant differences in the diets of immature and adult eagles, both fed preferentially on European Hare, and while immatures seemed to select areas of high hare density, adults did not. Although adults included a significantly greater proportion of birds in their diets, they did not show a preference for areas with higher bird densities, and they preferred rugged areas where the densities of birds were lower than on flat areas.

Vegetation height and density have been shown to affect the vulnerability of prey to raptors (Wakeley 1978, Baker

& Brooks 1981, Bechard 1982, Janes 1985, Preston 1990). We do not know the effect that differences in vegetation between rugged and flat areas might have had in the actual availability of hares to the eagles, but their effect should have been similar for both immature and adult eagles. Jiménez and Jaksic (1989), in an area of Chile where rodents (60–230 g) were the main prey, found that adult Grey Eagle-buzzards did not forage preferentially on areas of sparse vegetation. They also concluded that adult eagles selected foraging areas in relation to topography and not to prey density or availability.

The idea that differences in the distributions of immature and adult eagles result from differences in their foraging strategy is supported by the observation that adults use wing-flapping flight (which is more costly; Pennycuik 1989) less often than do immatures. Further, adults were able to fly with a lower wing-flapping frequency when flying over slopes than when flying over plains, while immatures always flew with a higher wing-flapping frequency than adults. Although our measures of flight performance were approximate, the differences observed between immature and adult eagles suggest that adults are able to save more energy than immatures when flying over slopes. Adults might be more skillful at slope soaring or their different shape might make them more capable of slope soaring with extremely light air updrafts.

The differences in morphology between immature and adult Grey Eagle-buzzards have not been studied in detail. Immatures have significantly longer tails than adults but a similar folded wing-length (Jiménez & Jaksic 1990, J. Bustamante *et al.*, unpubl. data). The observed difference in shape (Brown & Amadon 1968, Jiménez & Jaksic 1990) indicates that adults have wider wings than immatures. The distances from the leading edge to the trailing edge of the wing, measured midway between the wrist and the body, were 335 mm and 336 mm in two immatures and 350 mm and 370 mm in two eagles in almost full adult plumage that we measured in the study area. Probably these differences allow adult eagles to exploit air updrafts over rugged terrain more efficiently than do immatures. Our results suggest that adult eagles select foraging habitats in which the costs of foraging flights are lower while immatures cue on prey abundance.

We are very grateful to Miguel Angel Pineda, Martín Funes and Obdulio Monsalvo for help with the field work and to Titina Zapata for identifying the mammal hairs. Our thanks to Gerardo Aleña, Gabriel Anz, Miguel Anz, Raul Cordero and the administrators of the Estancias Quemquemtreu, Cerro de los Pinos, Collun-Co, Lolén, Collon-Curá, Pali-tué and Chimeuín, who permitted us to work on their land. Logistic support was provided by the Centro de Ecología Aplicada del Neuquén (Argentina); we thank Alejandro del Valle and Antonio Guinazú for their constant kind assistance. Financial support was provided by Instituto de Cooperación Iberoamericana and the Ministerio de Asuntos Exteriores (Spain) through the Programa de Cooperación Científica con Iberoamérica.



## REFERENCES

- Aitikin, A., Anderson, D., Francis, B. & Hinde, J. 1989. *Statistical Modelling in GLIM*. Oxford: Clarendon Press.
- Baker, J.A. & Brooks, R.J. 1981. Distribution patterns of raptors in relation to density of Meadow Voles. *Condor* 83: 42–47.
- Baker, R.J. 1987. *GLIM 3.77 Reference Manual*, 2nd ed. Oxford: Numerical Algorithms Group.
- Bechard, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. *Condor* 84: 153–159.
- Bennetts, R.E. & McClelland, B.R. 1991. Differences in the distribution of adult and immature Bald Eagles at an autumn concentration in Montana. *Northwest Sci.* 65: 223–230.
- Bohall-Wood, P. & Collopy, M.W. 1986. Abundance and habitat selection of two American Kestrel subspecies in north-central Florida. *Auk* 103: 557–563.
- Brown, L. & Amadon, D. 1968. *Eagles, Hawks and Falcons of the World*, 1989 ed. Secaucus, N.J.: The Wellfleet Press.
- Brunner, H. & Coman, B.J. 1974. *The Identification of Mammalian Hair*. Melbourne: Inkata Press.
- Cabrera, A.L. 1976. Regiones Fitogeográficas Argentinas. *Enciclopedia Argentina de agricultura y jardinería*, Vol. II. Buenos Aires: Editorial ACME S.A.C.I.
- Chehébar, C. & Martín, S. 1989. Guía para el reconocimiento microscópico de los pelos de los mamíferos de la Patagonia. *Doñana Acta Vert.* 16: 247–293.
- Crawley, M.J. 1993. *GLIM for Ecologists. Methods in ecology*. Oxford: Blackwell Scientific.
- Dobson, A.J. 1983. *Introduction to Statistical Modelling*. London: Chapman & Hall.
- Fretwell, E.D. & Lucas, H.L., Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19: 16–36.
- Hirald, F., Donazar, J.A., Ceballos, O., Travaini, A., Bustamante, J. & Funes, M. 1995. Breeding biology of a Grey Eagle-buzzard (*Geranoaetus melanoleucus*) population in Patagonia. *Wilson Bull.* 107: 675–685.
- Janes, S.W. 1985. Habitat selection in raptorial birds. In Cody, M.L. (ed.) *Habitat Selection in Birds*: 159–188. San Diego, Calif. Academic Press.
- Jiménez, J.E. & Jaksić, F.M. 1989. Behavioral ecology of Grey Eagle-buzzards, *Geranoaetus melanoleucus*, in central Chile. *Condor* 91: 913–921.
- Jiménez, J.E. & Jaksić, F.M. 1990. Historia natural del águila *Geranoaetus melanoleucus*: Una revisión. *Hornero* 13: 97–110.
- Koplin, J.R. 1973. Differential habitat use by sexes of American Kestrels wintering in northern California. *Raptor Res.* 7: 39–42.
- McCullagh, P. & Nelder, J.A. 1983. *Generalised Linear Modelling*. London: Chapman & Hall.
- Nelder, J.A. & Wedderburn, R.W.M. 1972. Generalised linear models. *J. R. Stat. Soc. A* 135: 370–384.
- Novaro, A.J., Capurro, A.F., Travaini, A., Funes, M.C. & Rabinovich, J.E. 1992. Pellet-count sampling based on spatial distribution—A case study of the European Hare in Patagonia. *Ecol. Austral* 2: 1–8.
- Pennycuik, C.J. 1989. *Bird Flight Performance—A practical calculation manual*. New York: Oxford University Press.
- Preston, C.R. 1980. Differential perch-site selection by color morphs of the Red-tailed Hawk (*Buteo jamaicensis*). *Auk* 97: 782–789.
- Preston, C.R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* 92: 107–112.
- Rosenzweig, M.L. 1985. Some theoretical aspects of habitat selection. In Cody, M.L. (ed.) *Habitat Selection in Birds*: 517–540. San Diego, Calif.: Academic Press.
- SAS Institute Inc. 1987. *SAS/STAT User's Guide*, Version 6. Vols 1 and 2, 4th ed. Cary, N.C.: SAS Institute Inc.
- Schipper, W.J.A., Buurma, L.S. & Bossenbroek, P. 1975. Comparative study of hunting behaviour of wintering Hen Harriers *Circus cyaneus* and Marsh Harriers *Circus aeruginosus*. *Ardea* 63: 1–29.
- Siegel, S. & Castellan, N.J., Jr. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
- Smallwood, J.A. 1987. Sexual segregation by habitat in American Kestrels wintering in southcentral Florida—Vegetative structure and responses to differential prey availability. *Condor* 89: 842–849.
- Stinson, C.H., Crawford, D.L. & Lauthner, J. 1981. Sex differences in winter habitat of American Kestrels in Georgia. *J. Field Ornithol.* 52: 29–35.
- Travaini, A., Donazar, J.A., Ceballos, O., Funes, M., Rodríguez, A., Bustamante, J., Delibes, M. & Hirald, F. 1994. Nest-site characteristics of four raptor species in the Argentinian Patagonia. *Wilson Bull.* 106: 753–757.
- Wakeley, J.S. 1978. Factors affecting the use of hunting sites by Ferruginous Hawk. *Condor* 80: 316–326.

Submitted 27 July 1995; revision accepted 14 April 1996