

## LONG-TERM STUDY OF A GOSHAWK BREEDING POPULATION ON A MEDITERRANEAN MOUNTAIN (ABRUZZI APENNINES, CENTRAL ITALY): DENSITY, BREEDING PERFORMANCE AND DIET

VINCENZO PENTERIANI

Laboratoire d'Ecologie, Université de Bourgogne, Batiment "Mirande," B.P. 400, 21011 Dijon Cédex, France  
and

Stazione Romana Osservazione e Protezione Uccelli, (S.R.O.P.U.), % Oasi Naturale W.W.F. "Bosco di Palo,"  
00055 Ladispoli, Rome, Italy

**ABSTRACT.**—The breeding density, breeding performance and breeding diet of a Mediterranean population of Goshawks (*Accipiter gentilis*) were studied in central Italy over a 10-yr period. Sixteen goshawk nesting pairs were found within a 318 km<sup>2</sup> area (5.03 pairs/100 km<sup>2</sup>). The minimum distance between pairs averaged 3.5 km. I observed a total of 51 nesting attempts at seven nest sites. Annual mean productivity of breeding pairs was 2.28 fledgings/successful pair and 1.69 fledgings/egg-laying pair. The occurrence of nesting failures was correlated with rainfall during April–May ( $r = 0.77$ ,  $P < 0.01$ ) and brood size at fledging was related to laying date ( $r = -0.71$ ,  $P < 0.05$ ). The diet included 20 species of birds (representing 75% of the prey and 71% of the biomass) and six species of mammals (representing 25% of the prey and 29% of the biomass). Wood Pigeon (*Columba palumbus*), Jay (*Garrulus glandarius*), Mistle Thrush (*Turdus viscivorus*), red squirrel (*Sciurus vulgaris*) and edible dormouse (*Glis glis*) accounted for 67% of all prey captures. In terms of biomass, Jays (20.76%), Wood Pigeons (16.03%), red squirrels (12.64%) and edible dormice (12.29%) were the dominant prey. I found 23 plucking sites on the ground (44.2%), 21 on rock with moss (40.4%), seven on tree stumps (13.5%) and one on the root of an uprooted tree (1.9%).

**KEY WORDS:** Goshawk; *Accipiter gentilis*; breeding density; breeding performance; breeding diet.

---

Un estudio de tiempo largo de población de cría en *Accipiter gentilis* en un Montaña Mediterráneo (Abruzzi Apennines, Centro de Italia): densidad, éxito de cría y dieta

**RESUMEN.**—Densidad de cría, éxito de cría y dieta de cría de la población en el Mediterráneo de *Accipiter gentilis* fueron estudiados e el centro de Italia arriba de un tiempo de 10 años. Decisies *Accipiter gentilis* pares con nidos fueron encontrados dentro de 318 km<sup>2</sup> (5.03 pares/100 km<sup>2</sup>). La distancia mínima entre pares fue 3.5 km. Yo observe un total de 51 intentos de poner nido en sieta sitios del nido. La productividad de promedio anual de pares en cría fue 2.28 pajaritos/pares con éxito y 1.69 pajaritos/huevo-ponido del par. La occurencia de nidos sin éxito fue correlacionado con lluvia durante abril-mayo ( $r = 0.77$ ,  $P < 0.01$ ). Al tiempo de poner ( $r = -0.71$ ,  $P < 0.05$ ). La dieta incluyo 20 especie de pajaros (representando 75% de presa y 71% de biomass) y seis especie mamiferos (representando 25% de la presa y 29% de la biomass). *Columba palumbus*, *Garrulus glandarius*, *Turdus viscivorus*, *Sciurus vulgaris*, y *Glis glis* dio cuenta por 67% de toda la presa. En referencia a biomass, *Garrulus glandarius* (20.76%), *Columba palumbus* (12.29%), fueron la presa dominante. Yo econtre 23 sitios de desplumar en el terreno (44.2%) 21 en pierdas con musgo (40.4%) sieta en un tronco de un arbol desarraigado (1.9%).

[Traducción de Raúl De La Garza, Jr.]

In Europe, most studies of Goshawks (*Accipiter gentilis*) have focused on northern and central European populations (Thiollay 1967, Opdam 1975, Opdam et al. 1977, Kos 1980, Marquiss and Newton 1982, Kalabér 1984, Wilke et al. 1985, Goszczynski and Pilatowski 1986, Bühler and Oggier 1987, Widén 1989, Anonymous 1990, Kostrzewa

and Kostrzewa 1990, Joubert 1991, Pielowski 1991, and Olech 1996). A few studies have attempted to estimate breeding densities in Mediterranean habitats but almost nothing is known concerning their food habits (Morillo and Lalanda 1972, Benussi and Perco 1984, Garrigues et al. 1990, Mañosa et al. 1990, Mañosa 1994).

The objectives of this study were to determine the breeding density of a Goshawk population on a Mediterranean mountain, to describe its breeding biology in the area, to show a possible relationship between weather and breeding success and to describe the breeding diet.

#### STUDY AREA AND METHODS

This study was conducted from 1984–93 in an area of the Apennine mountains in the Abruzzi region of central Italy (41°49'N, 13°47'E) that included Abruzzo National Park and the Sirente and Majella massifs. The area ranges in elevation between 800–2300 m and consists mostly of beech (*Fagus sylvatica*) forested slopes with grazed and fallow farmland at the base of the mountains. Above 1900 m, forests are replaced by high-altitude pastures.

I located Goshawk nest sites by searching forested areas mapped on 1:10 000 aerial photos and 1:25 000 topographic maps. Nest sites were located by walking through forests between November–April, observing nuptial displays and territorial flights (especially from the second week of March to the first week of April) and playback of taped calls. Occasionally, I found nests from pluckings, droppings and moulted feathers, and adult and nestling calls. Density of nesting pairs was estimated based on Newton et al. (1977). Regularity in nest-site spacing was computed using a G-test (Tjernberg 1985).

The breeding chronology and performance of Goshawks was studied from 1984–93 at seven nest sites. From the end of March until the end of April, nests were visited to determine occupancy, changes of site and egg-laying dates.

Occupied nests were observed from the end of May until fledging to determine nesting success. Counts of nestlings were done from the ground (the slope was always very steep, facilitating counts) or by watching the nest with a high-power telescope (60×).

I used the definitions of Kostrzewa and Kostrzewa (1990) and laying pairs were those pairs that laid eggs, successful pairs were those that fledged at least one chick and unsuccessful pairs were those that lost their clutches or nestlings at any stage before fledging.

The "Hydrographic Service" (Ministero dei Lavori Pubblici 1984–93) provided monthly values for total precipitation (mm) and mean temperatures from March–June. To investigate the relationship between spring weather and Goshawk breeding performance, weather data were examined for each month and for pairs of months (e.g., March–April, April–May and May–June; Kostrzewa and Kostrzewa 1990). Rainfall and temperature were used as statistically independent values.

From 1984–93, I collected prey remains and pellets near seven nests and known plucking sites throughout the breeding season to determine the diet of Goshawks. Prey remains and pellets were identified by macroscopic comparison with reference collections. For each vertebrate prey item identified, I attempted to identify both its species and whether it was an adult or juvenile. I determined age class based on the size, plumage, feather characteristics and degree of ossification in the prey remain. The biomass of each prey species was estimated by

using weight data from the study area or bibliographic material (Geroudet 1946–57). All pellets from individual visits were pooled. I recorded the species that occurred in samples but made no attempt to quantify the number of individuals in samples. To avoid counting the same prey twice in remains and pellets, prey in pellets were computed only if they had not been found as remains in the same visit (Mañosa 1994). Moreover, during each visit, an effort was made to remove all prey remains.

I studied use of different plucking sites by Goshawks. To do so, I assigned each prey remain to one of five categories: bare rock, rock with moss, ground, root of uprooted tree and tree stump. A single plucking site was counted only once if it had been repeatedly used by the species.

#### RESULTS

I found a total of 16 pairs of nesting Goshawks in the 318 km<sup>2</sup> study area for a density of 5.03 pairs/100 km<sup>2</sup>. Minimum distance between pairs averaged 3.5 km (range 2–4.9 km, SD = 1.02). A G-test value of 0.99 indicated that nest sites were distributed regularly.

Because I did not know of all seven breeding pairs at the beginning of the study, I observed a total of only 51 nesting attempts and collected detailed breeding data at only 43 nests over the 10-yr study period. Egg laying took place between the second and third week of April and fledging occurred between the first and second week of July. Eggs were laid during the first week of April at only one nest. Three nests fledged one young (7%), 20 fledged two young (46.5%) and 11 fledged three young (25.6%). In 9 cases (20.9%), the pairs failed to fledge a single young.

All of the nesting areas contained at least two nest structures at the time nesting was first initiated each year. Despite this, Goshawks usually used the same nest from one year to the next. Only in seven cases did they use alternate nests and in two cases they actually laid second clutches in the same nest.

Annual productivity was 2.28 fledgings/successful pair (SD = 0.41, range 1.75–2.75) and 1.69 fledgings/egg-laying pair (SD = 0.58, range 0.6–2.6). In 1991, only a single pair bred successfully fledging 3 young.

The percentage of unsuccessful pairs was correlated with rainfall during April–May which coincided with prelaying and laying, incubation and hatching periods ( $r = 0.77$ ,  $P < 0.01$ ). There was no relationship between percentage of unsuccessful pairs and temperature nor was there a relationship between percentage of fledged young per successful pair and May–June temperature or May–June

Table 1. Prey items found in the diet of Goshawks in the Abruzzi Apennines, Italy. Weights of prey are given in grams. Species with fewer than 10 individuals in the diet are listed as other birds.

	N (%)	TOTAL WEIGHT (%)
Birds	582 (73.76)	103 273 (72.1)
<i>Columba palumbus</i>	67 (8.49)	22 961 (16.03)
<i>Strix aluco</i>	13 (1.65)	6006 (4.19)
<i>Picus viridis</i>	17 (2.15)	3378 (2.36)
<i>Garrulus glandarius</i>	194 (24.59)	29 729 (20.76)
<i>Corvus c. cornix</i>	16 (2.03)	7760 (5.42)
<i>Turdus merula</i>	13 (1.65)	1066 (0.74)
<i>Turdus philomelos</i>	31 (3.93)	2790 (1.95)
<i>Turdus viscivorus</i>	108 (13.69)	12 028 (8.4)
Unidentified thrush	23 (2.91)	1736 (1.21)
Unidentified bird	61 (7.73)	
Other birds <sup>a</sup>	39 (4.94)	15 819 (15.32)
Mammals	200 (26.24)	39 956 (27.9)
<i>Sciurus vulgaris</i>	73 (9.25)	18 106 (12.64)
<i>Glis glis</i>	88 (11.15)	17 600 (12.29)
Unidentified mammals	31 (3.93)	
Other mammals <sup>b</sup>	39 (4.99)	4250 (4.11)
Total	782	123 160

<sup>a</sup> Other birds: *Buteo buteo* (nestlings), *Accipiter nisus*, *Falco tinnunculus*, *Columba livia*, unidentified pigeon, *Alectoris graeca*, *Picoides major*, unidentified woodpeckers, *Pica pica*, *Saxicola rubetra*, *Parus caeruleus*, *Carduelis chloris*, *Acanthis cannabina*, *Gallus domesticus*.

<sup>b</sup> Other mammals: unidentified mouse, unidentified shrew, *Lepus capensis*.

rainfall. The mean brood size at fledging was negatively correlated with laying date ( $r = -0.71$ ,  $P < 0.05$ ).

I identified a total of 782 prey items representing 26 different species in the diet of these Goshawks (Table 1). There were 20 species of birds (representing 75% of the prey and 71% of the biomass) and six species of mammals (representing 25% of the prey and 29% of the biomass). Wood Pigeons (*Columba palumbus*), Jays (*Garrulus glandarius*), Mistle Thrush (*Turdus viscivorus*), red squirrels (*Sciurus vulgaris*) and edible dormice (*Glis glis*) accounted for 67% of the identified prey. In terms of biomass, the Jay (20.76%), the Wood Pigeon (16.03%), red squirrel (12.64%) and edible dormouse (12.29%) were the dominant prey.

The total proportion of nestling birds ( $N = 51$ ) that occurred in the sample was 8.76%. Most of these were nestlings of crows ( $N = 28$ ), thrushes ( $N = 16$ ) and raptors ( $N = 7$ ).

I identified 52 plucking sites used by Goshawks.

Of these, 23 were on the ground (44.2%), 21 on rocks covered with moss (40.4%), seven on tree stumps (13.5%) and one on root of an uprooted tree (1.9%). No plucking sites were found on bare rock substrates.

#### DISCUSSION

I found the breeding population of Goshawks in the Abruzzi mountains to be very regular in its distribution with a density similar to that of other areas in Europe (5 pairs/100 km<sup>2</sup> in Finland, Wikman 1977; 4.5–5.5 pairs/100 km<sup>2</sup> in Germany, Kramer 1972, Link 1981, Dietrick and Ellenberg 1982; and 4.4 pairs/100 km<sup>2</sup> in Switzerland, Bühler and Oggier 1987).

Unlike other areas of Europe (Opdam 1975, Opdam et al. 1977, Rust and Kechele 1982, Kayser 1993) and other areas within the Mediterranean (Morillo and Lalanda 1972, Garrigues et al. 1990, Mañosa et al. 1990, Mañosa 1994) where Goshawks have very diverse diets, Goshawks in the Abruzzi Apennines had very low species diversity in their diet. This was probably related to the fact that the high elevation of the study area limited the numbers and types of bird species available (20 breeding species with a density of 36 pairs/10 ha, Bernoni 1995) compared to the neighboring, lower-elevation piedmont (59.2 pairs/10 ha, Pandolfi and Taferna 1991) and plain (158 pairs/10 ha, Bernoni et al. 1989). At lower elevations, land use was also more varied and habitats were more productive resulting in a greater diversity of prey species. Similar Goshawk diets dominated by a few prey species have been reported in coniferous forests in Sweden (Widén 1989), higher altitudes in Britain (Marquiss and Newton 1982), mountains of France (Joubert 1991), and woodlands in north-eastern Italy (Benussi and Perco 1984).

Crows (27.25%), thrushes (22.18%), medium-sized rodents (20.4%) and pigeons (9.63%) were the most frequently taken as prey. A large portion of the diet also consisted of nestlings, most of which were crows. Crows, thrushes, pigeons, medium-sized rodents and nestlings have also been reported in the diets of Goshawks in Europe (Höglund 1964, Sulkava 1964, Opdam et al. 1977, Goszczynski and Pilatowski 1986, Widén 1989, Mañosa et al. 1990, Kayser 1993, Mañosa 1994) and in other regions (Reynolds and Meslow 1984, Boal and Mannan 1994). The abundance of forest species such as Wood Pigeons, Jays, red squirrels and edible dormice in the diet indicates that these Gos-

hawks hunt inside or at the edges of woodlands (Opdam et al. 1977).

The productivity of Goshawks in the Abruzzi Apennines was more typical of the productivity that has been observed in bad years in forested areas in Lorraine and Limous regions of France (Thiollay 1967, Nore 1977), in Finland (Cramp and Simmons 1980), in high elevation areas in Britain (Marquiss and Newton 1982), in southern Bavaria (Rust and Kechele 1982), in the eastern part of the Swiss Lowlands (Bühler et al. 1987) and in Catalunya (Mañosa et al. 1990). Productivity in the Abruzzi Apennines was heavily weather dependent. During cold, wet springs breeding started later and prolonged rain reduced reproductive success possibly by decreasing hunting success and food intake. Rainfall appeared to be a very significant factor. During the breeding season of 1991, nearly all the nesting attempts failed owing to intense rainfall during the incubation period. The highest incidence of nest failure occurred when there was between 60–120 mm of rain. The negative impact of rainfall on Goshawk populations has also been stressed by Kostrzewa and Kostrzewa (1990). Based on the correlation between weather and nest failures, laying date and mean brood size upon fledging, April and May appeared to be critical in the breeding cycle. Forest cutting during April and May also had a marked negative effect on the productivity of Goshawks. Forests were cut in the vicinity of five nesting areas during this period. At all five areas, the nesting attempt failed that year. By contrast, forest cutting at four nesting areas during the last three weeks prior to fledging had no effect on the breeding success.

#### ACKNOWLEDGMENTS

I am indebted to Fabio Liberatori for his invaluable cooperation in the field throughout the study period and to Gianni Marangoni for his precious help in determining the prey remains. I also thank Marina Cerasoli and Francesco Pinchera who contributed to the search of the sites, as well as M. Chiavetta, Mr. Pellegrini, Ms. Pellegrini, M. Garfagnini, M. Bernoni, the Caramanico Terme and Rocca di Mezzo Forest Stations. The Administration of the Abruzzi National Park partially provided logistic and financial support for this work. I thank especially F. Tassi, the Director and C. Sulli. I thank Bruno Faivre, Bernard Frochot, Patrick Giraudoux and Jean Secondi for their indepth review of the manuscript. Stefania Sarceni kindly helped with the English translation.

#### LITERATURE CITED

- ANONYMOUS. 1990. Breeding biology of Goshawks in lowland Britain. *Brit. Birds* 83:527–540.
- BENUSSI, E. AND F. PERCO. 1984. Osservazioni eco-etologiche sull'Astore *Accipiter g. gentilis* nel carso triestino. *U.D.I.* 9:3–25.
- BERNONI, M., L. IANNIELLO AND P. PLINI. 1989. Censimento dell'avifauna nidificante in un bosco deciduo dell'Italia centrale. *Avocetta* 13:25–29.
- . 1995. Il metodo del mappaggio in una faggeta del Parco Nazionale d'Abruzzo. *Avocetta* 19:131.
- BOAL, C.W. AND R.W. MANNAN. 1994. Northern Goshawk diets in a ponderosa pine forest on the Kaibab Plateau. Pages 97–102 in W.M. Block, M.L. Morrison and M.H. Reiser [Eds.], *The Northern Goshawk: ecology and management. Stud. Avian Biol. No. 16.*
- BÜHLER, U. AND P.A. OGGIER. 1987. Bestand und bestandsentwicklung des habichts *Accipiter gentilis* in der Schweiz. *Ornithol. Beob.* 84:71–94.
- , R. KLAUS AND W. SCHLOSSER. 1987. Brutbestand und jungenproduktion des habichts *Accipiter gentilis* in der Nordostschweiz 1979–1984. *Ornithol. Beob.* 84:95–110.
- CRAMP, S. AND K.E.L. SIMMONS. 1980. *Handbook of the birds of Europe, the Middle East and North Africa.* Vol. 2. Oxford Univ. Press, Oxford, UK.
- DIETRICK, J. AND H. ELLENBERG. 1982. Aspects of Goshawk urban ecology. Pages 163–175 in R.E. Kenward and I.M. Lindsay [Eds.], *Understanding the Goshawk.* I.A.F., Oxford, UK.
- GARRIGUES, R., R. MARTINEZ AND J.A. MORATA. 1990. Introducción al estudio de la biología del azor (*Accipiter gentilis* L., 1758) en Albacete. *Al-basit, Rev. Estud. Al-bacetenses* 27:123–162.
- GEROUDET, P. 1946–1957. *La vie des oiseaux.* Vols. 1–6. Collection de Poche. Les Beautés de la Nature. Delachaux et Niestlé S.A., Paris, France.
- GOSZCZYNSKI, J. AND T. PILATOWSKI. 1986. Diet of Common Buzzard (*Buteo buteo* L.) and Goshawks (*Accipiter gentilis* L.) in the nesting period. *Ekol. Pol.* 34:655–667.
- HÖGLUND, N.H. 1964. Über die Ernährung des Habichts (*Accipiter gentilis* Lin.) in Schweden. *Viltrevy* 2:271–328.
- JOUBERT, B. 1991. Questions sur la chronologie de la reproduction chez l'Autour des palombes (*Accipiter gentilis*) en Haute-Loire. *Nos Oiseaux* 41:39–54.
- KALABÉR, L. 1984. Note sulla biologia e lo sviluppo postembrionale dell'Astore, *Accipiter gentilis*, in Romania. *Riv. Ital. Ornitol.* 54:179–190.
- KAYSER, Y. 1993. Le régime alimentaire de l'Autour des palombes, *Accipiter gentilis* (L.), en Alsace. *Ciconia* 17. 143–166.
- KOS, R. 1980. Der habicht in der bundesrepublik Deutschland. *Vögelwelt* 101:161–175.
- KOSTRZEWA, A. AND R. KOSTRZEWA. 1990. The relationship of spring and summer weather with density and breeding performance of the Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis* and Kestrel *Falco tinnunculus*. *Ibis* 132:550–559.
- KRAMER, V. 1972. *Habicht und sperber.* Wittenberg-Lutherstadt, Berlin, Germany.

- LINK, H. 1981. Zur situation des habichts im Frankischen Raum im Vergleich zu anderen mitteleuropaischen populationen. *Okol. Vogel.* 3:221-226.
- MAÑOSA, S. 1994. Goshawk diet in a mediterranean area of northeastern Spain. *J. Raptor Res.* 28:84-92.
- , J. REAL AND E. SANCHEZ. 1990. Comparació de l'ecologia de dues poblacions d'astor *Accipiter gentilis* a Catalunya: el Vallès Moianès i la Segarra. *El Medi Natural del Vallès* 2:204-212.
- MARQUISS, M. AND I. NEWTON. 1982. The Goshawk in Britain. *Br. Birds* 75:243-260.
- MINISTERO DEI LAVORI PUBBLICI. 1984-93. Annali idrologici. Sezione autonoma del genio Civile, Bacini con foce al litorale tirrenico dal salinello al fortore. Servizio Idrografico.
- MORILLO, C. AND J. LALANDA. 1972. Primeros datos sobre la ecología de las Falconiformes en los montes de Toledo. *Bol. Estac. Cent. Ecol.* 2:57-70.
- NEWTON I., M. MARQUISS, D.N. WEIR AND D. MOSS. 1977. Spacing of Sparrowhawk nesting territories. *J. Anim. Ecol.* 46:425-441.
- NORE, T. 1977. L'Autour et l'épervier en Limousin. *Ornithol. Limousin* 7:25-41.
- OLECH, B. 1996. Anthropogenic food of the Goshawk as a factor influencing the breeding phenology. Page 37 in M. Pandolfi [Ed.], 2nd International Conference on Raptors, Urbino, Italy.
- OPDAM, P. 1975. Inter- and intraspecific differentiation with respect to feeding ecology in two sympatric species of the genus *Accipiter*. *Ardea* 63:30-54.
- , J. THISSEN, P. VERSCHUREN AND G. MÜSKENS. 1977. Feeding ecology of a population of Goshawk *Accipiter gentilis*. *J. Ornithol.* 118:35-51.
- PANDOLFI, M. AND G. TAFERNA. 1991. Censimento del popolamento di Passeriformi di un bosco di conifere e di uno di latifoglie dell'Italia centrale. Pages 375-378 in M. Fasola [Ed.], Atti II Seminario Italiano Censimenti Faunistici dei Vertebrati. *Suppl. Ric. Biol. Selvaggina*, XVI:1-820.
- PIELOWSKI, Z. 1991. Liczebność populacji i efekty legów ptaków drapieżnych w krajobrazie rolniczym okolic Czempinia (zach. Polska). *Acta Ornithol.* 26:107-118.
- REYNOLDS, R.T. AND E.C. MESLOW. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. *Auk* 101:761-779.
- RUST, V.R. AND W. KECHELE. 1982. Ergebnisse langjähriger Bestandkontrollen beim habicht (*Accipiter gentilis*) auf zwei südbayerischen Kontrollflächen. *Garmischer vogelkd. Ber.* 11:10-26.
- SULKAVA, S. 1964. Zur nahrungsbilogie des habichts, *Accipiter gentilis* (L.). *Aquilo, Ser. Zool.* 3:1-103.
- THIOLLAY, J.M. 1967. Ecologie d'une population de rapaces diurnes en Lorraine. *Terre Vie* 21:116-183.
- TJERNBERG, M. 1985. Spacing of Golden Eagle *Aquila chrysaetos* nests in relation to nest site and food availability. *Ibis* 127: 250-255.
- WIDÉN, P. 1989. The hunting habitats of Goshawks *Accipiter gentilis* in boreal forests of central Sweden. *Ibis* 131: 205-231.
- WIKMAN, H. 1977. Duvhokspredation pa skogsfagel i sydastra Finland 1975-1976. Foredrag fra Nordisk skogfuglsymposium: 59-72. Direktoratet for vilt of fersk vannfisk, Viltrappot 5.
- WILKE M., A. GOTTMANN AND H.G. SCHNEIDER. 1985. Beutetiere des habichts (*Accipiter gentilis*) auf drei nordhessischen Untersuchungsflächen. *Vogelkd.* 11:69-77.

Received 8 March 1997; accepted 10 August 1997