

Mervyn Griffiths, 1978: The biology of the *Monotremes*. Academic Press, New York, San Francisco, London, str. VIII+367, cena — 31 dolarów USA.

Monotremata, zwierzęta odkryte dopiero w XVIII wieku, interesowały głównie embriologów i anatomów. Dopiero w ciągu ostatnich 20 lat nastąpił nagły napływ badań fizjologicznych, biochemicznych, ekologicznych, behawioralnych i paleontologicznych. Biologia stekowców jest niezwykle interesująca, chociażby ze względu na ich prymitywne gadzio-ssące cechy, na niewyjaśnione dotąd ich filogenetyczne pochodzenie i wreszcie, że znajomość biologii współcześnie żyjących *Monotremata* może pomóc w zrozumieniu biologii ssaków mezozoicznych, których szkielety kranialne i postkranialne mają wiele wspólnych cech z ówczesnie żyjącymi stekowcami.

Treść książki ujęto w 10 rozdziałów. W każdym kolejno omówiono: dziobaka, kołczatkę i prakolczatkę. Wiadomości dotyczące prakolczatki są dość skąpe, jako, że gatunek ten jest najsłabiej poznany.

Niedawna jeszcze historia odkrycia stekowców oraz ich ogólna charakterystyka jest tematem pierwszego rozdziału. Dokładnie omówiono budowę szkieletu wraz z jego rozwojem embrionalnym. Zwrócono uwagę na cechy gadzie i ssące chondrocranium oraz porównano szkielet stekowców ze szkieletem wymarłych ssaków mezozoicznych.

W rozdziale 2 przedstawiono różnicowanie wewnętrzzgatunkowe stekowców, rozmięszczenie geograficzne, terytorializm. Szczegółowo omówiono morfologię, anatomię i fizjologię gruczołów udowych *Monotremata*. Gruczoły te u dziobaka wydzielają jadowitą substancję o silnie toksycznym działaniu. W okresie godowym samce eksponują ostrogi gruczołów i w ten sposób ostrzegają i odstraszają inności samców od samic po cechach zewnętrznych oraz określono stosunek płci w obserwowanych, wolnożyjących populacjach stekowców. Na podstawie analizy elektroforetycznej wykazano istnienie polimorfizmu hemoglobiny kołczatek pochodzących z różnych terenów Australii.

Zagadnienia związane z odżywianiem się stekowców opisano w rozdziale trzecim. U dziobaka, którego pokarmem są wodne bezkręgowce wyjaśniono sezonowe zmiany ilości zapasowego tłuszczu nagromadzonego w ogonie. Przedstawiono morfologiczne przystosowanie kołczatek odżywiających się mrówkami i terminami do zdobywania i przyswajania tego specyficznego pokarmu. Próbowano wyjaśnić, dlaczego kołczatki na jednych terenach preferują mrówki, a na innych termity mimo, że oba owady są na równi dostępne. Na temat pożywienia prakolczatki niewiele dotąd wiadomo. Prawdopodobnie głównym, jeśli nie jedynym jej pokarmem są dżdżownice.

Rozdział 4, zatytułowany „Rozmaitości fizjologiczne” jest faktycznie zbiorem różnych wiadomości z fizjologii stekowców. Między innymi opisano: budowę i pracę serca, budowę naczyń krwionośnych, obieg krwi, skład morfologiczny krwi, pracę nerek, wymianę gazową w płucach, przystosowanie dziobaka do nurkowania.

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Feeding Ecology of the Spanish Lynx in the Coto Doñana

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Delibes M., 1980: Feeding ecology of the Spanish lynx in the Coto Doñana. *Acta theriol.*, 25, 24: 309-324 [With 5 Tables & 1 Fig.]

To study the food habits of the Spanish lynx were analysed 1537 droppings collected throughout two periods of one year in Doñana, S. W. Spain. A food test which was carried out on a captive lynx allowed us to relate the number of occurrences of each kind of prey in the samples with the actual numbers of individual preys and the biomass devoured. The main prey is the rabbit which amounts to 79% of the prey captured and 85% of the biomass consumed. The next in importance are the ducks (9% and 7% respectively) and the ungulates (3% and 5%). Seasonal variations in the diet are not very pronounced. The importance of rabbits is at its maximum between July and October, that of the ducks between March and June and that of the cervids between November and February. The prey is selected for the facility in which they may be caught rather than for their abundance. It is estimated that an individual lynx consumes about 74 gr of food per kilo of body weight daily. The impact of the predation on the prey populations is difficult to evaluate, but it seems to be very important on the fallow deer population, relatively important on these of rabbits and red deer and very slight on that of ducks. Predation on ungulates in the study area may be a kind of starvation-related mortality.

[Est. Biol. Doñana, C.S.I.C., Paraguay 1, Sevilla 12, Spain]

1. INTRODUCTION

The Spanish lynx, *Lynx pardina* (Temminck, 1824), whose specific identity has recently been upheld by Kurtén (1968) and van den Brink (1970) by demonstrating that in the past it has coexisted sympatrically with the European lynx, *Lynx lynx* (Linnaeus, 1758), is one of the most characteristic predators of the Iberian Mediterranean ecosystems. Despite this, its ecology and biology are not well known, mainly due to its small area of distribution and its rarity, since it is a seriously endangered species (I.U.C.N., 1978). The only works published until present on the food habits of this species, include some field observations compiled by Valverde (1957, 1963, 1967), the analysis of a few gut contents and faeces by Delibes et al. (1975), Delibes (1975) and Palma (1977) and the paper by Rogers (1978), in which are presented, incorrectly in some aspects, some of my unpublished data.

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In this paper information is given on the composition of the food of lynxes and its seasonal fluctuations, discussing the main factors which influence the diet and the pressure of the predator on prey populations. This should allow some progress in getting to know the role of this endangered species in the Iberian Mediterranean biocoenoses.

2. STUDY AREA

The study was carried out in the Biological Reserve of Doñana, property of the Spanish National Council for Scientific Research (C.S.I.C.). This Reserve includes 68 km² inside the limits of the Doñana National Park, situated on the right bank of the mouth of the River Guadalquivir (approximately 37° N, 6° 30' W). The altitude above sea level varies from between 0 m to 32 m. The "marismas" which are usually flooded from October–November to May–June, cover approximately 84% of the area. The maquis, a dense thicket of *Halimium* spp., *Erica* spp., *Juniperus phoenicea* Linnaeus, 1753, *Arbutus unedo* Linnaeus, 1753, etc., with some rather scattered cork-oak trees (*Quercus suber* Linnaeus, 1753) and pines (*Pinus pinea* Linnaeus, 1753) a few permanent lakes and numerous temporary pools, cover approximately 60% of the area. Dense plantations of pines cover 26%, and the remaining 6% is sand dunes with sparse vegetation. A more detailed description of the area is to be found in Allier et al. (1974). The lynxes and their prey usually inhabit the maquis, especially the ecotones maquis-marismas and maquis-lagoons where there are abundant pastures.

The climate of the region is mediterranean with a slight atlantic influence. The summers are warm and dry and the winters mild and wet. The average annual rainfall is about 500 mm, 87% of which falls between October and April. During the study period, severe autumnal droughts delayed the appearance of the herb layer affecting seriously herbivores populations.

3. MATERIAL AND METHODS

3.1. Material

The diet was assessed by the analysis of faeces. From February 1973 to February 1974 and from October 1975 to October 1976, about 2,000 droppings were collected in the study area. More than 400 were rejected as there was some doubt as to whether they were of the lynx or some other carnivore species. Consequently, I worked with 1,337 lynx faeces. The results obtained month by month throughout the two years do not differ statistically and therefore both years have been combined. The smallest sample corresponds to December (97 droppings) and the largest to March (221 droppings). The study of animals killed or devoured by free-living and captive lynxes has supplied the information about the consumption of preys.

3.2. Method of Analysis of Faeces

The individual excrements were dissociated in water to separate their components (hair, feathers, bones, etc) which were identified as closely as possible to the species level by using a reference collection.

Usually, the results of the analysis of faeces are shown simply as the frequency

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of occurrence of particular constituents, a method which at times seems to be the most practical and suitable (Erllinge, 1968; Krulik, 1972). Often, however, this procedure offers only an approximate idea of the diet of the predator, particularly if the preys are of varied size or nature (Mech, 1970). Because of this, it has been tried for some time to relate dropping content to prey consumed (Scott, 1941), usually looking for the ratio of consumed food weight to remnants weight in faeces (Lockie, 1959; Goszczyński, 1974). Due to some practical difficulties and mainly because various faeces had been partially consumed by dung beetles, whose differential action on the constituents of these is unknown, we have therefore used a somewhat different method, in some respects similar to that recently devised for the study of the wolf (*Canis lupus* Linnaeus, 1758) by Floyd et al. (1978). This method consists in relating the number of occurrences of each type of prey in the faeces with the actual number of individuals and the biomass consumed from this type of prey.

3.3. Food Tests

The experiments were carried out with an apparently adult female lynx weighing about 8 kg. She was kept in a cage of 3X2X2 m with an attached hut of 1X0.5X0.5 m. For 68 consecutive days, this animal was fed (only 6 days a week) with natural prey. The proportions of the various prey types used were approximately similar to those which, according to preliminary studies, might occur in the diet of lynxes in the wild. The prey was weighed and offered dead to the lynx at nightfall, usually only once a day. The following morning, the uneaten remains were collected and weighed. The excrements produced were collected individually twice a day. The rabbits *Oryctolagus cuniculus* (Linnaeus,

Table 1
Results of the food test carried out with a captive lynx for 68 consecutive days.

Prey species	N	Biomass consumed, g	Avg. biomass consumed per indiv.	No. of occurrences of droppings	Avg. number of occurrences of droppings per individual
Rabbit (<i>Oryctolagus cuniculus</i>)	50	9000	180	...	...
Fawn (<i>Cervus europaeus</i>)	1	1250	1250	4	4
Small rodents	2	77	approx. 40	3	1.5
Norwegian rat (<i>Rattus norvegicus</i>)	1	130	130	2	2
Mallard (<i>Anas platyrhynchos</i>)	4	2008	approx. 500	15	3.75
Partridge (<i>Alectoris rufa</i>)	1	360	360	2	2
Magpie (<i>Pica pica</i>)	1	130	130	2	2

1758) used in the experiment were collected at random in the study area and their weight varied between 300–1400 g, averaging 807 ± 29 g (n=52). It is assumed that the size distribution of the rabbits consumed by free-living lynxes is similar. The fawn carcass was kept in the cage for only 24 hours, as there is no known cases of the Spanish lynx eating twice from the same prey (Valverde, 1957; Delibes, 1977; Palma, 1977). This criterion could be a probable source of error, as we shall discuss later on (see 4.4.).

The results of the tests are shown in Table 1 where we also show the indices

Table 2
Results of the analysis of the 1537 droppings.

Prey species	Number of occurrences	Frequency of occurrence	Percent of occurrence
MAMMALIA			
<i>Lepus capensis</i>	4	0.26	0.22
<i>Oryctolagus cuniculus</i>	1358	88.35	73.21
<i>Lagomorpha</i> (unidentified)	5	0.33	0.27
<i>Elomys quercinus</i>	12	0.78	0.65
<i>Rattus</i> sp.	6	0.39	0.32
<i>Arvicola sapidus</i>	1	0.07	0.05
<i>Apodemus-Mus</i> spp.	19	1.24	0.05
Small mammals (unident.)	14	0.91	1.02
<i>Cervus elaphus</i>	18	1.17	0.75
<i>Dama dama</i>	48	3.12	0.97
Ungulates (unidentified)	16	1.04	2.59
AVES			0.86
<i>Anas platyrhynchos</i>	204	13.27	11.00
<i>Anas crecca</i>	7	0.46	0.38
<i>Anas strepera</i>	4	0.26	0.22
<i>Anas penelope</i>	1	0.07	0.05
<i>Anatidae</i> (unidentified)	56	3.64	3.02
<i>Alectoris rufa</i>	31	2.02	1.67
<i>Coturnix coturnix</i>	1	0.07	0.05
<i>Gallinula chloropus</i>	2	0.13	0.11
<i>Fulica atra</i>	2	0.13	0.11
<i>Rallidae</i> (unidentified)	3	0.20	0.16
<i>Columba</i> sp.	1	0.07	0.05
<i>Strigidae</i> (<i>Athene noctua</i> ?)	1	0.07	0.05
<i>Turdus merula</i>	1	0.07	0.05
<i>Pica pica</i>	3	0.13	0.16
<i>Passeriformes</i> (unidentified)	3	0.13	0.16
Birds (unidentified)	33	2.15	1.78
REPTILIA			
<i>Elaphe scalaris</i>	1	0.07	0.05
TOTAL	1855	—	99.93
OTHER REMAINS (not food)			
Lynx hairs	187		
Mongoose hairs	1		
Insecta	39		
Faecal pellets of deer	51		
Vegetal matter	185		

As to the deer faecal pellets and the vegetal remains, they must have been ingested accidentally by the predator together with some food. All these remains are incorrectly included as prey species by Rogers (1978).

4.2. Seasonal Fluctuations in Diet

Although the rabbit plays an important part in the diet throughout the whole year, there are appreciable seasonal fluctuations, both considering the number of individual prey captured and the biomass consumed (Fig. 1). These fluctuations are clearer if the year is divided into

which relate for each type of prey the number of occurrences with the actual number of individual preys and the biomass consumed. The index of the mallard (*Anas platyrhynchos* Linnaeus, 1758) will be used for all the *Anatidae*, the index of the red deer fawn (*Cervus elaphus* Linnaeus, 1758) for all the ungulates and the magpie *Pica pica* (Linnaeus, 1758) index for all the birds (including unidentified ones), with the exception of ducks and red-legged partridges *Alectoris rufa* (Linnaeus, 1758).

The described method is certainly open to criticism as its reliability depends on numerous assumptions. In spite of this, I think it is possible to interpret the results much more precisely than by simply showing the data of frequency of occurrence.

4. RESULTS AND DISCUSSION

4.1. Prey Species

The food of the lynx is not very varied and is based on the rabbit, whose remains appear in more than 88% of the samples (Table 2). Although a minimum of 21 species of vertebrates have been found in the diet, only two, the rabbit and the mallard, occur in more than 5% of the faeces and only six [the previously mentioned plus the red deer and fallow deer *Dama dama* (Linnaeus, 1758), the red-legged partridge and the *Apodemus-Mus*] in more than 1%.

Among the unidentified *Anatidae* there is probably some greylag goose *Anser anser* (Linnaeus, 1758), as wild lynxes have been observed eating this prey on three occasions. Also, among the unidentified ungulates, some young wild boar (*Sus scrofa* Linnaeus, 1758) can be represented, as lynxes have sometimes been seen in Doñana carrying young wild boar in the mouth (Valverde, 1967).

In short, the Spanish lynx is primarily a predator of mammals (80.9% of the total occurrences) and secondarily of birds (19%), with a monotonous diet despite the fact that it occasionally captures different preys including reptiles [as well as the ladder snake *Elaphe scalaris* (Schinz, 1822) reported on here, we can add an eyed lizard *Lacerta lepida* Latham, 1802, found in one stomach by Delibes et al., 1975]. The capturing of cattle (sheep, goats, calves) seems to be exceptional (Valverde, 1957; Delibes et al., 1975). In relation to the diet of the lynx in other European and American localities, the small role played by hares (*Lepus* spp.) is noteworthy; in Spain these are preyed upon very seldom by *Lynx pardina*, due mainly to the fact that the two species occupy different habitats.

Some remains have not been considered as food (Table 2). Mongooses *Herpestes ichneumon* (Linnaeus, 1758), as other carnivores, are usually killed but not eaten by the lynx in Doñana, while the insects found in droppings were probably previously consumed by the prey themselves.

three periods: spring (from March to June inclusive), summer (from July to October) and autumn-winter (from November to February) (Table 3). The frequencies of occurrence of the various kinds of prey in the three periods considered have been compared by means of the chi-square test (Table 4). The most striking seasonal changes occur in the consumption of rabbits, ungulates and ducks.

4.2.1. Rabbits

There is a strong negative correlation between the relative frequency of rabbits in the diet each month, and the corresponding trophic diversity (Delibes, 1977). This suggests that rabbits are the favourite prey, probably more ducks and ungulates being consumed when the availability of rabbits diminishes. Brand *et al.* (1976) find this type

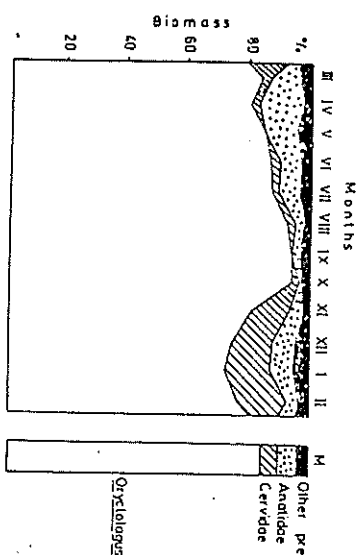


Fig. 1. The food of the lynx along the year, expressed as percentages on the estimated biomass consumed every month. M = Annual average.

of functional responses to changes in the abundance of favourite prey in *Lynx canadensis* Kerr, 1792, and Beasom & Moore (1977) in *Lynx rufus* (Güldenstaedt, 1776).

During the study period, the representative season of the favours in the area was from January to July (Delibes & Calderón, 1979). This produced a peak in the number of this species in May-June a very marked decline in summer (caused by scarcity of food due to the summer drought, by mixomatosis and probably by predation) and a minimum in December-January. The density in May-June can be three or more times higher than in October. As rabbits are more consumed from July to October this means that the seasonal variations of the consumption of rabbits do not agree with the corresponding variations in the density of this prey. This could be attributed to two things:

- an increase in the availability of rabbits in summer (irrespective of their abundance) motivated by the vulnerability of the young and

above all, of those suffering from mixomatosis, as this disease affects rabbits in Spain almost exclusively in summer.

b) a case of «switching» — a phenomenon defined as «a flexible search image» or «the ability of a general predator to become a conditioned to its more abundant prey species, so that the number of attacks on it are disproportionately greater than would be expected by chance encounters» (Cornell, 1976). In our case, the conditioning would occur

Table 3

Seasonal variations in the food, expressed as the frequency of occurrence of every type of prey (P.O.), the percent on the estimated number of captured prey (P.P.) and the percent on the estimated consumed biomass (P.B.). The annual average has been computed with the percentages of every month.

March-June, n=562			July-Oct., n=458			Nov.-Febr., n=517			Annual avg., n=1537		
P.O.	P.P.	P.B.	P.O.	P.P.	P.B.	P.O.	P.P.	P.B.	P.O.	P.P.	P.B.
87.4	75.4	84.1	95.6	87.5	92.9	83.0	74.2	76.7	88.5	79.2	84.7
2.3	1.0	2.1	0.7	0.4	0.7	12.8	6.3	13.8	5.3	2.6	5.4
3.0	5.1	1.1	2.2	2.5	0.6	5.0	6.0	0.9	3.3	4.1	0.8
27.9	13.7	10.9	9.8	5.4	4.1	13.5	7.2	6.3	17.4	8.9	7.1
5.3	4.9	1.7	4.1	4.2	1.7	6.4	6.3	2.3	5.3	5.2	2.0
125.9	100.1	99.9	112.4	100.0	100.0	120.7	100.0	100.0	119.8	100.0	100.0
Total			Total			Total			Total		

in May-June when the density of rabbits is greater, and its effects last throughout the summer, including October.

From October, the number of rabbits in the field is low and almost all the individuals are adults and healthy. Only then must the lynx look for alternative prey, the most important of which in autumn-winter are the ungulates.

4.2.2. Ungulates

In the study area we found 13 carcasses of deer killed by lynxes. Of these, 10 were of fawns (6 fallow deer and 4 red deer) and only three of adults (all fallow deer: two females and one 3 years-old male with symptoms of disease). This proportion (77% fawns over the total cervids) can be assumed, but it probably gives less value to the part played by infants which are captured in an even higher proportion. The calving season of red deer and fallow deer in Doñana lasts from the end of April to the middle of June and therefore does not coincide with the maximum consumption of fawns which occurs in autumn-winter. This could be partly due to the greater availability of rabbits

from May, and also to a probable increase in the vulnerability of the fawns after the mating season of the adults (in September-October), when the materno-filial bond is weakened and the protection provided by the mother to the young diministes (Lent, 1974). Alvarez et al. (1975) have described the defensive behaviour of adult female fallow deer accompanied by infants when faced with the Spanish lynx. Apart from this, there is no doubt that the severe drought of the autumns of 1973, 1974 and 1975 made the cervids much more vulnerable, as some of them even died of starvation.

Table 4

Comparison of the frequencies of occurrence of the various prey in the three periods by the chi-square test.
+++ = $p < 0.001$; ++ = $p < 0.05$; — = $p > 0.05$

	Rabbits	Ungulates	Ducks	Other Mammals	Other Birds
(March—June)/(July—Oct.)	+++	+	+++	—	—
(July—Oct.)/(Nov.—Febr.)	+++	+++	—	+	—
(Nov.—Febr.)/(March—June)	+	+++	+++	—	—

Although systematic studies have not been carried out, it seems that since 1976 the predation of the lynx on the ungulates has diminished notably in the area.

4.2.3. Ducks

From March to May the principal food source alternative were the ducks, especially *Anas platyrhynchos*. In this period many mallards leave the marshes in order to mate and to nest in the small pools of the maquis. During the mating period many of them walk on dry ground and are very noisy both during the night and day, being therefore a very vulnerable prey. Again, the vulnerability is more important than the abundance in determining the intensity of predation, as the greatest density of waterfowl in the area is reached during the winter, from October to February.

4.3. Food Requirements

In order to discuss the impact of the lynx on the populations of preys it is necessary to know not only the relative frequencies of each type of prey in the diet, but also the absolute quantities which each individual kills and uses. This is difficult as the data available often comes from animals in captivity, and individual differences also play an important part.

Our captive lynx which was fed in the conditions mentioned in section 3.3., remained in good physical condition consuming 40,199 g in 68 days. This means 591 g/day which represents about 7.4% of body weight (74 g/kg/day). It is considered that this intake, halfway between the maximum values estimated for other species of the genus *Lynx* of similar body weight (Saunders, 1963; Colley et al., 1965; Brand et al., 1976), could be a valid approximation to the average intake of a free-living individual Spanish lynx.

4.4. Annual Consumption per Individual

Knowing the average biomass taken daily by an individual lynx, it is possible to find the total biomass consumed in one year, which will then be distributed among the different kinds of prey according to the percentages summarised in the last column of Table 3. Admitting that the average biomass consumed of each individual prey agree with the values obtained in the food-test (column 3 in Table 1), we can calculate the approximate number of individual preys killed and consumed by a lynx in one year (Table 5).

As indicated in 3.3. the number of ungulates in Table 5 should be

Table 5

Estimated consumption per individual lynx in Doñana.

Prey	Biomass/year, kg	No. individuals/year, approx.
Rabbits	182.711	261
Ungulates	11.649	9
Other Mammals	1.726	14 (1 hare)
Ducks	15.316	31
Other Birds	4.134	19 (7 partridges)
Total	215.536	334

considered with caution. Due to the fact that the captive lynx only used 1250 g of the fawn carcass offered in the test, a total annual consumption of less than 12 kg of ungulates corresponds to the capture of 9 individual deer. This estimation would be considerably lower if any one of the following circumstances would occur: (a) the lynx eat from the deer carcass again after having eaten from it once, as frequently shown by other species of the genus, (b) various individual lynxes eat from the same carcass, (c) a single lynx takes more than 1250 g in one feeding session, (d) the Spanish lynx eat carrion.

Of all these possibilities, (a) and (d) have not been confirmed

but (b) and (c) certainly occur in occasions. Thus, the figures in Table 5 must be valid approximations to the annual consumption per individual lynx with regard to rabbits, other mammals, ducks and other birds. In the case of ungulates, however, the estimation is an extreme value, perhaps several times greater than the actual figure.

4.5. Effect of Lynxes on Prey Populations

There is no reliable information of the numbers and dynamics of the lynx population and its prey, so the following results are very speculative and are only a basic approach to the problem.

4.5.1. The Number of Lynxes

From direct observations and sand prints there is evidence that in 1973 there were 4 female lynxes with kittens in the study area (perhaps 5), although two of these partly occupied peripheral areas. In other years the number of reproductive females was less (in 1976 only one was seen, but my searching effort was less). For the calculations, I have arbitrarily taken 10 as the average number of lynxes living in the study area. This is probably a low estimation.

4.5.2. Impact on Rabbits

The number of rabbits in the area are not well known. Transect counts by Rogers (1974) in different biotopes and seasons in 1973 should be regarded — according to the author — as indices rather than estimates of absolute population densities. The same kind of direct counts have been made by Sorigner (pers. com.) in the autumn of 1976. The indices are expressed however as individuals per km² which allows us to generalize them over the whole area. The average resulting standing crop in September–October is between 2,000 and 3,000 individuals.

Supposing that the monthly changes in the numbers and the monthly rate of disappearance are similar in Doñana to those found by Sorigner (1979) in a population of rabbits 100 km to the north, the standing crop previously mentioned should correspond approximately to a total number of discrete individuals present over a year equalling 75,000. Predation by the lynxes therefore would affect annually 3.5% of the total number of rabbits which occupy the area.

Although the percentage obtained is low, the impact of the lynx on rabbit population may be important. Many adult and subadult individuals with a high reproductive value are captured. Also, the pressure of

predation is stronger from July to October, when the numbers of rabbits are low. Predation by lynx during such a period may modify the rate of reconstruction of population numbers, as Gośczyński (1974) indicates for the predation by *Vulpes vulpes* on *Microtus arvalis* (Pallas, 1779) in Poland.

4.5.3. Impact on Ungulates

Predation by the lynx seems to have no influence on the populations of wild boar, which are controlled at present by diseases, specially the swine fever.

Let us assume that an individual lynx kills 9 individual ungulates each year though this is an over-estimation (see 4.4.). All the lynxes will kill 90 ungulates per year and if all these are red deer and fallow deer and the proportion of the former to the latter is 1:2.66, (Table 2) the result is approximately 26 red deer and 74 fallow deer. According to the proportion of sexes and ages of the carcasses found (see 4.2) all the red deer will be fawns (again this is an over simplification, as some adult females are captured; Valverde, 1967; Alvarez et al., 1975), and among fallow deer there must be 67% fawns, 22% adult females and 11% non-fawn males. The number of cervids preyed upon annually would therefore be 26 red deer fawns, 50 fallow deer fawns, 16 adult females fallow deer and 8 non-fawn male fallow deer.

The average standing-crop of fallow deer in 1973 was 217, of which 123 were adult females and 37 non-fawn males (Brazá, 1975). I do not know the average length of residence of individuals during the year, but the total number of fallow deer present can be estimated at approximately 150 adult females and 50 non-fawn males. The approximate annual production would be 120 fawns. Predation would therefore affect 120% of the non-fawns and 41% of the newborn each year.

There is no estimation available of the size of the red deer population living in the area. Rogers' data (1974) based on direct censuses allows us to presume that in the autumn the proportion of red deer to fallow deer is 1.5:1. However, the red deer is certainly underestimated as it is more scattered in the area and is found in more covered areas than the fallow deer, being for this reason more difficult to make a direct census even in selected seasons. If the number of red deer is double that of fallow deer, the lynx would be responsible for the loss of about 10% of the fawns red deer born each year.

As in the area the lynx is the only predator of cervids, and the populations of these, specially that of fallow deer, seem to be food and habitat-limited there, many of the individuals killed by the predator probably would die from other causes if there were no lynxes

(»compensatory predation«, Errington, 1967). Supporting this hypothesis is the fact that 4 of 6 fawns (red and fallow deer) killed by the lynx were completely lacking fat in their bone marrow, which points to a physical condition near to starvation (Cheatum in Mech, 1970).

4.5.4. Impact on Ducks

The marshes of the Guadalquivir are the annual wintering quarters for 100,000 to 150,000 *Anatidae* (Sánchez, 1975) and the breeding ground for 5,000 pairs of mallards and lesser numbers of other species (Aguiar-Amat, pers. com.). Only a small fraction of these actually occupy the study area, but in any case the impact of the lynx need not be given much importance.

4.5.5. Impact on Other Preys

The impact of the lynx on the populations of small mammals is negligible as very few individuals are captured. The predation on partridges affects less than 1% of the annual production.

5. CONCLUSIONS

The results of this study on the diet of the Spanish lynx confirm previous data of Valverde (1957, 1963, 1967), Delibes (1975), Delibes *et al.* (1975) and other authors. As with other species of the genus, *Lynx pardina* appears as a medium-sized predator specialized in the capture of homeothermic vertebrates, especially mammals. The basic prey is the rabbit. The Spanish lynx differs from the European lynx whose basic food are hares (*i.e.*, in Finland, Pulliainen & Hyypä, 1975; in Poland, Sumiński, 1973; etc.) or ungulates (*i.e.*, in Sweden, Haglund, 1966; in Altai, U.S.S.R., Novikov, 1962; in Czechoslovakia, Heil, 1975; in Rumania, Vasiliu & Decei, 1964, etc.).

Apparently the lynx population responded to the increase in rabbit availability by concentrating their food gathering efforts on this prey. When it is relatively difficult to catch rabbits, lynxes have to turn to a more varied diet, including mainly ducks or ungulates. Availability of the different preys depends less on their relative abundance than on the facility to capture them, which appears to be a common kind of response among many large and medium size carnivores (Schöener, 1971).

Although the actual figures presented in this study relating to the magnitude of the impact on prey populations are only approximate,

lynxes appeared to be an important source of mortality in rabbit, red deer and specially fallow deer populations, but it is not known what impact this mortality had on the densities of these prey species. In the case of the ungulates, predation may be a form of starvation-related mortality. In the case of the rabbits, the lynx appears to behave at the end of summer and in autumn as a no »prudent« predator (Slobodkin, 1968), exercising a great pressure of predation on specimens with a high reproductive value, which could limit the rate of reconstruction of the numbers of prey populations.

Predation on deer is age-selective, disproportionately more fawns being killed. Old animals are not selected, most probably because of being too large. There is also evidence that even among fawns predation is not at random, the sick and the weak being selected. This is opposed to the point of view of Bergerud (1971) who states that »with lynx, this kind of culling is largely absent« and confirms the results of Hornocker (1970), who supplies evidence for non-random selection by another »stalker«, the puma *Felis concolor* (Linnaeus, 1771) (for a discussion on the stalker-courser dichotomy of prey selection, see Schaller, 1972, and Curio, 1976). As Curio (1976) points out with reference to the puma, this supposes that the perceptual powers of assessing the vulnerability of prey by lynx are extraordinarily good. The lynx can probably prey selectively on the deer in Doñana because after the extinction of the wolf there does not exist any other coursing carnivore which does so (Schaller, 1972).

Finally, in the future it will be necessary to improve methods of censusing of rabbits and lynxes, to study the dynamics of ungulates populations and to determine carefully the patterns by which deer carcasses are used. Only in this way can the impact of predation be correctly established.

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STOSUNKI POKARMOWE *LYNX PARDINA* W COTO DOÑANA

Streszczenie

Stosunki pokarmowe *Lynx pardina* badano na podstawie 1537 prób kału zebra-
nych w ciągu 2 sezonów jednego roku, w południowo-zachodniej Hiszpanii (Ta-
bela 2). Test pokarmowy przeprowadzony na rysiu trzymanym w niewoli pozwolił
na porównanie ilości każdego rodzaju zdobyczy występującej w próbach z rze-
czywistymi ilościami odpowiedniej zdobyczy i zjadanej biomasy (Tabela 1).
Główną zdobyczą rysia są króliki stanowiące do 79% łowionych zwierząt i 85%
zjadanej biomasy. Następne są kaczki (odpowiednio 9% i 7%) i kopytne (3% i 5%).
Sezonowe zmiany w diecie są słabo wyrażone (Rycina 1). Króliki są najstot-
niejszym składnikiem pokarmowym od lipca do października, kaczki od marca
do czerwca, jeleniowate od listopada do lutego (Tabela 3, 4). Zdobyć jest wy-
bierana raczej pod kątem łatwości pozyskania niż obfitości. Oszacowano, że jeden
rys zjada około 74 g pokarmu na 1 kg ciężaru ciała na dobę (Tabela 5). Wpływ
drapieżnika na populację ofiary jest trudny do ustalenia, ale wydaje się być
bardzo ważny w przypadku populacji daniela, stosunkowo ważny dla populacji
królika i jelenia i niewielki dla populacji kaczek. Drapieżnictwo w stosunku do
kopytnych na badanym terenie może być związane z ich śmiertelnością wyni-
kającą z wygłodzenia.

The Diet and Growth of Fox Cubs in Two Regions of Scotland

H. H. KOLB & R. HEWSON

Kolb H. H. & Hewson R., 1980: The diet and growth of fox cubs in two regions of Scotland. *Acta theriol.*, 25, 25: 325—331 [With 3 Tables & 2 Figs.]

Analysis of stomach contents showed that in North-east Scotland fox cubs are mainly fed on rabbits and hares, whereas in the West of Scotland they are fed on lambs and voles. The rate of growth of litters is the same in the two regions, but cubs in the West are born on average between a week and a fortnight later than those in the North-east. It is suggested that this is due to different periods of availability of the main foods in the two habitats.

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I. INTRODUCTION

Foxes *Vulpes vulpes* (Linnaeus, 1758) live in a great variety of habitats and eat a wide range of foods. The way in which populations adapt to these local circumstances is poorly understood. Previous work on foxes in Scotland has described the food, changes in density and reproductive condition of adults (Kolb & Hewson, 1979, 1980). This paper presents some information on the diet, date of birth and growth of fox cubs in two parts of Scotland and discusses the possible role of food availability in determining variations in the breeding and development of foxes.

II. MATERIAL AND METHODS

Litters of cubs killed during normal fox control operations were collected from gamekeepers, forestry rangers and shepherds between 1971 and 1976. One sample came from North-east Scotland (Grampian), an area of moorland, forestry and lowland farming. The other came from the West of Scotland (Strathclyde and parts of Central and Highland), an area of forestry, upland sheep farming and deer forest. No significant differences were found in diet or growth within these areas so that they represent two homogeneous samples from either side of Scotland (see Fig. 1, Kolb & Hewson, 1979).

All data came from litters killed on a known date. Each cub was weighed and measured from the top of the snout to the root of the tail (head and body length). The animal was then autopsied and its stomach contents identified as described in Kolb & Hewson (1979). In the analysis of diets the litter was taken as the sampling unit. Results are presented as the percentage frequency

