

# POST-FLEDGING DEPENDENCE PERIOD AND DEVELOPMENT OF FLIGHT AND FORAGING BEHAVIOUR IN THE EGYPTIAN VULTURE *Neophron percnopterus*

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**ABSTRACT** In northern Spain the first flights of fledgling Egyptian Vultures *Neophron percnopterus* took place between 28 July and 28 August (at the age of 68-80 d). The post-fledging period ended between 29 August and 5 September when the young migrated (at the age of 89-113 d). The length of the post-fledging period was between 9-34 days and correlated negatively with the date of first flight. The number of flights carried out per day, the flight duration, the time spent flying, the time spent soaring and the size of the home range increased with age. Older fledglings in broods of two were more precocious and active in flight than their siblings. Early self-feeding both on carrion not brought by parents and on food pirated from other Egyptian Vulture nests was observed. The young followed their parents during their visits to feeding places; this behaviour is unusual among raptors and may be related with maturation of social foraging strategies.

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## INTRODUCTION

Information on the length of post-fledging and the development of behavioural patterns during that period has been gathered for numerous species of birds of prey (see eg. Kussman 1976, Sherrod 1983, Gonzalez *et al.* 1985, Willie 1985, Alonso *et al.* 1987, Lett & Bird 1987, Walker 1987, Bustamante & Hiraldo 1989). Nonetheless, with the exception of the study by Robertson (1985) information on Old World vultures is very limited. Therefore, prevailing opinions about the length of the post-fledging period and the age at which young are self-sufficient are speculative. Brown & Amadon (1968) maintained that after attaining flight, young vultures should be capable of searching for carcasses and feeding by themselves, rapidly becoming independent while Newton (1979) and Mundy (1982) suggested there is prolonged parental care due to the need to obtain a scarce and unpredictable food resource (see also O'Connor 1984). In this paper we describe the phenology and length of post-fledging period in the Egyptian Vulture *Neophron*

*percnopterus* together with the development of flight and foraging behaviour during this period.

## STUDY AREA AND METHODS

The study was carried in the Bardenas Reales region, Ebro valley, Navarra (northern Spain). The relief is predominantly flat and around 400 m a.s.l. It has a cold mediterranean climate (Aschmann 1973). The population of Egyptian Vultures (40 pairs) is stable and reaches one of the highest densities in Europe (14.5 km<sup>2</sup>/pair).

The observations were made during July, August and September 1986 and 1987. Eight fledglings were studied; for six of them we knew the dates of the first flight and of the migration; five of these fledglings were monitored continuously along the whole post-fledging period; they belonged to two broods of two (VE86 and LC87) and one brood of one (GL87). All the fledglings were fitted with wing tags (Kochert *et al.* 1983) and radiotransmitters fixed with a backpack harness. Radiotransmit-

ters weighed 15-20 g and did not noticeably affect the behaviour of the fledglings (pers. obs.). The observations were made from fixed points at 200-400 m away. They started a week before the probable date of the first flight and ended with the migration or the death of the fledgling. The number of days of observations was VE86 = 16, LC87 = 26, GL87 = 13, other nests (total) = 11. Each day the observations extended from dawn to dusk (05.00-20.00 GMT). Two teams made simultaneous observations at each nest recording the fledglings' behaviour and their movements both in the vicinity of the nest and outside of the territory.

The development of flight skills was determined using the following variables:

- (1) N FLIGHT: Number of flight initiated per day.
- (2) DUR FLIGHT: Average daily duration of the flight, in seconds.
- (3) TM FLIGHT: Daily time spent in flight (in hours).
- (4) TM FLAPP: Daily percentage of time spent in flapping flight, with respect to the total time flying.
- (5) TM GLID: Daily percentage of time spent in gliding flight, with respect to the total time flying.
- (6) TM SOAR: Daily percentage of time spent in soaring flights, with respect to the total time flying.
- (7) HOME RANGE: Daily size of the home range (ha) calculated by the minimum convex polygon method, excluding the day of departure on migration.
- (8) TM PR-FL HR: Time spent daily by the fledg-

ling in company with the parents outside of the territory (in hours).

The changes in the values of these variables in relation to the age of the fledglings were tested by two different ways. Firstly fledgling age in five ten-day age periods (65-74, 75-84, 85-94, 95-104 and 105-114) was considered. For each of these periods the middle value and standard deviation was calculated for each variable considering daily information from all the fledglings together. Secondly moment-product correlations (Sokal & Rohlf 1969) were calculated between age and each of the variables both for all the chicks combined and for each of the five chicks for which more than ten days of observations evenly spread over the post-fledging period had been made. For each of the two double broods studied the differences between siblings in the mean values for each variable throughout all the post-fledging period were tested. The age of the fledglings was accurately known from a growth study carried out with these very chicks (Donázar & Ceballos 1989).

## RESULTS AND DISCUSSION

### Phenology and length of the post-fledging period

Table 1 summarizes the results obtained. The first flights of the fledglings took place between

**Table 1.** Dates and age (days) of first flights, first soaring and migration departure of fledglings studied. The length (days) of the post-fledging period is also indicated. In double broods the older (F-1) and younger (F-2) siblings are distinguished. The fledgling CT87 was killed by a red fox when 82 days old.

Fledgling	flight		soaring	Migration		
	Date	Age	Age	Date	Age	PF period
LC86	28-Aug.	80	83	05-Sep.	89	19
VE86(F-1)	30-Jul.	77	80	04-Sep.	113	36
VE86(F-2)	07-Aug.	80	82	29-Aug.	102	22
LC87(F-1)	28-Jul.	72	82	03-Sep.	109	37
LC87(F-2)	07-Aug.	77	92	03-Sep.	104	27
GL87	30-Jul.	68	97	01-Sep.	101	33
CT87	19-Aug.	71	-	-	-	-

28 July and 28 August when they were 68-80 days old (mean = 75,  $n = 7$ ). The fledglings' departure on migration occurred between 29 August and 5 September when they were 89-113 days old (mean = 103,  $n = 6$ ). The length of the post-fledging period thus varied between 9 and 37 days (mean = 28,  $n = 6$ ) being negatively correlated with the date of the first flight ( $r_4 = -0.970, p < 0.001$ ). In the two double broods studied (VE86 and LC87) the second-hatched chicks were older than their siblings when they flew (3 and 5 days respectively). However the second-hatched chicks were younger when they migrated (VE86 = 11 d, LC87 = 5 d). The six fledglings studied and two other fledglings that were observed less systematically migrated before and independently of their parents. In the nest LC87 the parents set off on migration five days (for the male) and seven days (for the female) after the chicks, which left together.

The results show that while the period in which the first flights of the fledglings spans more than a month, the migratory departures are restricted to one week. These findings, and the absence of a correlation between these dates and the acquisition of the ability to undertake long range flights with soaring suggests that, as in other migratory raptors (Bustamante & Hiraldo 1989) the length of the post-fledging period of the Egyptian Vulture is independent of the flying abilities of the fledgling and is only determined by the date when the first flight occurs, with which variable it is significantly negatively correlated.

The shortness of the dependence period of the Egyptian Vulture is surprising when longer parental care might have been expected given the body size of the species (see Newton 1979 for comparisons) and the scarcity and unpredictability of the food resources of the vultures (Newton 1979, O'Connor 1984). In fact, Old and New World vultures seem to have very long dependence periods (see Koford 1953, Jackson 1975, Anthony 1976, Mundy 1982) although in some large species as the Cape Vulture *Gyps coprotheres* and the Cinereous Vulture *Aegyptius monachus* the length of the post-fledging period appears to be surprisingly variable (Robertson 1985, F. Hiraldo pers. comm.). It might

be argued that the short post-fledging period of the Egyptian Vulture could be due, as with other birds of prey (Newton 1979, Mader 1981, Sherrod 1983) to the necessity to migrate soon after the first flights. In all events, migration is not necessarily an obstacle to keeping parent-offspring ties since families migrating together could keep together in the wintering areas as appears to occur in other birds relying on food resources which are scarce or require considerable skills to secure (Ashmole & Tovar 1968, Feare 1975, Scott 1980). However our results indicate that the fledglings and their

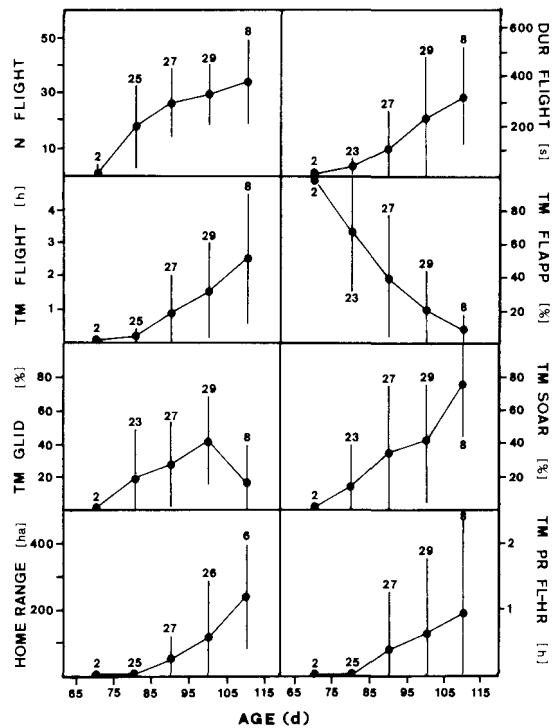


Fig. 1. Relationship between fledgling age and the variables considered (see Methods for meaning of abbreviations). For each period of ten days the mean and standard deviation (vertical bars) and the number of days of observation are indicated. Table 1. Dates and age (days) of first flights, first soaring and migration departure of fledglings studied. The length (days) of the post-fledging period is also indicated. In double broods the older (F-1) and younger (F-2) siblings are distinguished. The fledgling CT87 was killed by a red fox when 82 days old.

# SPRING CRANE *Grus grus* MIGRATION THROUGH GALLOCANTA, SPAIN

## II. TIMING AND PATTERN OF DAILY DEPARTURES

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**ABSTRACT** The relationships between the daily pattern of Common Crane *Grus grus* migration departures from a staging area and variables related to weather and number of birds were studied during 1984 and 1985 (totalizing 30 days with migration) using multivariate statistical analysis. Cranes left the roost to the foraging areas between 0628 and 0715 hours. On 95% of the days with migration, the departure lasted only 71-111 minutes, generally between 0900 and 1200 hours. The timing of departure was highly correlated with air temperature at departure initiation: cranes departed earlier with higher temperatures, probably as soon as thermal updrafts had developed and facilitated soaring flight. When the number of birds departing was higher due to favourable weather conditions, the departure evenness, flock size and number of flyways used increased, and the departure interval was slightly extended through an advancement of the initial time of departure.

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### INTRODUCTION

Severe weather during migration has probably been an important selection pressure favouring adaptive physiological and behavioural strategies in birds (see Alerstam 1978). Relationships between various weather variables and the day to day variations in migration volume have been demonstrated often (Richardson 1978 and references in Alonso *et al.* 1990). However, few papers have dealt with the diurnal pattern of migration, especially in relation to proximate factors such as weather (see Alerstam & Bauer 1973, Alerstam 1975, Pennycuick 1975, Pennycuick *et al.* 1979, Karlsson & Swanberg 1984, Swanberg 1987). Assuming the success of a migratory flight depends at least in part on the timing and pattern of migration initiation from a stopover locality, the study of relationships between these variables may be relevant to understanding the selective forces acting on migration.

In this paper the relationships between weather

and non-weather variables on the timing and pattern of migration departure are explored using multivariate statistical analysis, and the latter's possible effects on the success of a migratory flight are discussed.

### METHODS

We observed visible spring migration of Cranes at Gallocanta lake, Spain (40°58'N, 1°30'W). In this paper we consider the sample of 30 days in which migration occurred during the migratory periods February-March 1984 and 1985 (total 66 days). Details of the study area and general observation methodology are given in Alonso *et al.* 1990. The timing of migration departure was defined by four variables: (a) the initial departure time, (b) the mean departure time, (c) the final departure time, and (d) the departure interval, defined as (c) - (a). Variables (a), (b) and (c) were measured as the times in minutes after sunrise at which respectively

parents always leave separately on migration which make the retention of family bonds in the wintering areas scarcely feasible (Newton 1979).

### Development of flight skills

Considering the six fledglings studied as a single sample, the number of flights per day, the average flight length and the time spent flying tended to increase significantly with increased fledgling age (Fig. 1 and Table 2). Considering each fledgling independently, most correlations for these variables were significant, especially those referring to the average flight duration and the percentage of time spent flying. Soaring flight began when the fledglings were 80-97 days old (mean = 85.8,  $n = 6$ ) and progressively replaced gliding and flapping flight. In the days subsequent to abandoning the nest flapping flight dominated while gliding flight was relatively more frequent in the middle of the post-fledging period (Fig. 1). Thus, the age

of the fledgling tended to be negatively correlated with the frequency of flapping and positively with the frequency of soaring both for all the fledglings pooled together and for most of individual young (Table 2). There was no significant correlation between the age of the first soaring flight and the age of the first flight ( $r_4 = -0.632, p > 0.05$ ) or migratory departure ( $r_4 = -0.771, p > 0.05$ ). In double broods, the younger fledglings made their first soaring at a greater age than their older siblings (VE86 = 2 d, LC87 = 10 d). In general, the older siblings were much more active than their younger siblings as shown by comparison of the values of the variables (Table 3). The flights of older siblings were more frequent and prolonged; they employed more often the soaring flight whereas the younger siblings flapped more frequently.

Improvement in flight skills with age was in general parallel in all the fledglings studied and appeared to follow a similar trend to that found in

**Table 2.** Correlation coefficients of the variables selected with fledgling age (see Methods for meaning of abbreviations). Only values corresponding to days after the first flight were considered. In double broods the values of the older (F-1) and the younger (F-2) fledglings are shown. Degrees of freedom (number of days of observation) are in parentheses. \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .

Variable	Total	Nest					
		VE86		LC87		GL87	
		F-1	F-2	F-1	F-2		
N FLIGHT	0.38*** (89)	0.11 (14)	0.76** (10)	0.30 (22)	0.49* (17)	0.54 (11)	
DUR FLIGHT	0.55*** (87)	0.22 (14)	0.52 (10)	0.71*** (21)	0.64** (16)	0.59* (11)	
TM FLIGHT	0.58*** (89)	0.34 (14)	0.69* (10)	0.70*** (22)	0.65** (17)	0.64* (11)	
TM FLAPP	-0.63*** (87)	-0.66** (14)	-0.72** (10)	-0.62** (21)	-0.85*** (16)	-0.75** (11)	
TM GLID	0.13 (87)	-0.16 (14)	0.78** (10)	-0.26 (21)	0.32 (16)	0.42 (11)	
TM SOAR	0.52*** (87)	0.35 (14)	0.22 (10)	0.65*** (21)	0.69*** (16)	0.58* (11)	
HOME RANGE	0.51*** (84)	0.65** (13)	0.66* (9)	0.52* (21)	0.51* (16)	-0.08 (10)	
TM PR-FL HR	0.31** (89)	-0.03 (14)	0.49 (10)	0.52* (22)	0.43 (17)	0.26 (11)	

**Table 3.** Values recorded for fledglings from two double broods for each of the variables considered (see Methods for meaning of abbreviations). For each fledgling and variable the mean, the standard deviation (*SD*), *t*-value, degrees of freedom (*df*, number of days of observation 2) are presented. Differences were calculated using Student *t*-test. \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .

Variable	F-1		F-2		<i>t</i>	<i>df</i>
	mean	<i>SE</i>	mean	<i>SE</i>		
VE86						
N FLIGHT	27.3	9.2	21.5	10.5	1.55	26
DUR FLIGHT	237.5	194.2	75.0	64.1	2.55*	26
TM FLIGHT	12.0	8.5	3.3	3.3	3.08**	26
TM FLAPP	8.6	8.0	46.3	41.0	3.59**	26
TM GLID	23.6	22.4	31.1	33.9	0.70	26
TM SOAR	67.8	25.3	25.1	32.3	3.92***	26
HOME RANGE	143.2	140.1	16.6	30.3	2.67*	24
TM PR-FL HR	0.7	0.9	0.1	0.2	2.26*	26
LC87						
N FLIGHT	33.2	13.5	19.5	12.0	3.50**	41
DUR FLIGHT	180.3	200.7	187.7	291.9	0.09	40
TM FLIGHT	9.6	11.1	6.1	10.1	1.01	41
TM FLAPP	27.2	29.2	48.7	43.4	1.89	40
TM GLID	34.8	28.4	27.2	32.0	0.80	40
TM SOAR	38.9	38.7	23.2	36.9	1.32	40
HOME RANGE	113.0	185.0	24.5	62.2	1.84	39
TM PR-FL HR	0.7	1.1	0.4	1.1	0.88	41

fledglings of other birds of prey (see Brown 1966, Gargett 1972, Kussman 1976, Johnson 1986, Alonso *et al* 1987, Real & Mañosa 1987, Walker 1987, Bustamante & Hiraldo 1989). Egyptian Vultures fly when their primary length is around 84% of the adult length (Donázar & Ceballos 1989) feather growth continuing even after the first flight, as with other birds of prey (Bustamante & Hiraldo 1989). Thus the wing loading of the fledgling gradually diminishes so that soaring flight becomes progressively more feasible. The start of soaring flight appears occur at a relatively young age (80-97 days) so that even those fledglings which fly later (the last week of August) have sufficient time available to gain adequate flight skills for migration. The finding that the younger fledglings in double broods undertook the first flight and acqui-

red the ability to soar at a later age than their siblings could be due to the gap between siblings in feather growth, since the second-hatched chicks in double broods reach the necessary feather length for flight when eight days older on average than their siblings (range 3-14,  $n = 6$ , pers. obs.) (see also Donázar & Ceballos 1989).

#### Development of foraging and other behaviour

Throughout the entire post-fledging period the fledglings largely depended on their parents for food. Of all the feedings observed ( $n = 149$ ) 146 were items brought in the bill by adults and three were regurgitations. All feedings were in the nest except five which took place less than fifty meters away from it.

An early development of self-feeding was

shown. Thus the older sibling of the nest VE86 was seen eating rabbit *Oryctolagus cuniculus* carrion, not brought by the adults, on six different days first performing this behaviour when 86 days old. Self-feeding was also seen in two chicks from single broods which were not regularly followed but never in the two younger chicks of double broods. On the other hand some chicks appeared to develop very early skills of piracy shown on the visits they made to other Egyptian Vulture nests where they robbed food from the resident fledglings (Donázár & Ceballos in press). Two of the six fledglings studied (the siblings of the nest VE86) showed this behaviour, which we observed from an age of 80 days.

The size of the home range used by the fledglings tended to increase progressively with age (Fig 1 and Table 2). Very often the course of the fledglings followed that of their own parents so the time they spent away from the natal territory with their parents also increased progressively with age (Fig 1 and Table 2). At the beginning of the post-fledging period the fledglings only accompanied the adults for short journeys but as they perfected their powers of flight they followed the adults all the time they were outside the territory visiting feeding areas.

The fledglings sometimes showed adult behaviour. Thus on one occasion the older fledgling of a double brood fed its sibling with a small scrap of food picked up in the nest. Attacks were observed by resident fledglings towards intruding adult, immature and fledgling Egyptian Vultures. These attacks always took place when the intruder was perched next to the fledglings. The fledglings never tried to attack intruding Egyptian Vultures in flight probably because their flying skills were less well developed than in the intruders.

Early self sufficiency of fledglings in obtaining food appears to be rare in birds of prey with elaborate hunting techniques (see Brown 1966, Gargett 1972, Sherrod 1983) but relatively frequent when fledglings can feed on carrion when this is highly available (Mendelssohn & Leshen 1983, Wallace & Temple 1983, Walker 1987, 1988). In our study area the post-fledging period of the Egyptian

Vulture coincides with the irruption of the myxomatosis epizootic which kills a great number of rabbits every summer in the Mediterranean ecosystems (Soriguer 1981). For this reason, the early trophic self sufficiency of the fledglings may be favoured. Another technique for acquiring food which requires less skill is piracy at other nests. Kleptoparasitism by fledgling raptors on other nests are known to develop at early ages (see Johnson 1986) but in the case of the Egyptian Vulture, the piracy requires that neighbouring nesting territories are very close (Donázár & Ceballos in press). On the other hand, the appearance of typical adult behaviour (feeding, territory defence) during the post-fledging period of the Egyptian Vulture is not surprising since this phenomenon has been reported for numerous raptor species (Cade 1953, Brown 1976, Rosenfield & Kanvic 1983, Sherrod 1983, Gonzalez *et al* 1985, F. Hiraldo pers. comm.).

Perhaps our most interesting result was the attachment of young to their parents during their foraging trips. Fledglings of other birds of prey follow hunting adults (Newton 1979, 1987, Johnson 1986) but normally this behaviour seems to be adaptive to intercept the adult bringing prey to the nest, or to directly obtain prey from the adult as it is killed (see Meinertzhagen 1954, Sherrod 1983). This is not so for Egyptian Vultures, since all the feedings observed took place in the nest or its immediate vicinity. It is most surprising that the association between fledglings and parents becomes more frequent at the end of the post-fledging period when the rupture of familiar trophic bonds is almost completed and the fledglings are self-sufficient at carrion. For this reason, we think that the adaptive significance of this behaviour could be based mainly on the need to perfect foraging strategies that require close observation of other individuals. The mastering of these techniques (local enhancement, information transfer) which appear to be used by other vulture and large carrion eating eagles (Knight & Knight 1983, Rabenold 1983, 1987) could be particularly valuable for the Egyptian Vulture given that breeding adults are relatively social at carrion (Cramp & Simmons 1980) and that non-breeding birds tend to form communal

roost in breeding and wintering areas (Cramp & Simmons 1980, Ceballos & Donázar in press). Nonetheless it may be noted that other raptor species which seem to use these foraging techniques like the Bald Eagle *Haliaeetus leucocephalus*, the Black Kite *Milvus migrans* and the Cinereous Vulture do not show an analogous degree of association between parents and fledglings (Kussman 1976, Bustamante & Hiraldo 1989, F. Hiraldo pers. comm.). The only raptors known similarly to keep in contact with adults appear to be some New World vultures (see Wallace & Temple 1983). These authors found that the wild fledgling Black Vultures *Coragyps atratus* obtain some trophic advantages foraging together with their parents but released hand-reared fledglings of the same age were also capable to feed and survive by themselves suggesting that long periods of association with parents may be related with social adjustments.

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## SAMENVATTING

Dit artikel beschrijft de ontwikkeling van uitgevlogen jongen van de Aasgier. Zes van deze jongen konden langdurig worden gevolgd omdat zij waren gemerkt en voorzien van een zendertje. Het onderzoek vond plaats in de Ebro vallei (Noord Spanje). Plaatselijk komen daar de hoogste dichtheden van Aasgieren voor van Europa. Aandacht is besteed aan de duur van de periode waarin de jongen van de ouders afhankelijk zijn en aan de ontwikkeling van het vlieg- en foerageergedrag.

Tussen 28 juli en 28 augustus begonnen de jongen te vliegen, op een leeftijd van 68 tot 80 dagen. De periode van afhankelijkheid eindigde als de jongen uit het gebied wegtrrokken, tussen 29 augustus en 5 september, op een leeftijd van 89-113 dagen. De afhankelijkheidsperiode duurde van 9 tot 37 dagen (Tabel 1). Naarmate de jongen later in het seizoen waren uitgevlogen, duurde deze periode korter. Als de leeftijd toeneemt wordt per dag meer gevlogen (meer vluchten, langere vluchten, vliegtijd per dag langer), het aandeel van de zweefvluchten neemt toe en het leefgebied wordt groter (Fig. 1, Tabel 2). De oudste jongen in nesten van twee jongen, bleken zelfstandiger en actiever dan de jongste (Tabel 3).

Uitgevlogen jongen die nog door hun ouders werden verzorgd, bleken ten dele hun eigen voedsel te kunnen bemachtigen: aas en voedsel buitgemaakt uit nesten van andere Aasgieren. De jongen volgden hun ouders naar de voedselgebieden. Dit gedrag is ongewoon bij andere roofvogels. Het zou in verband gebracht kunnen worden met de ontwikkeling van een sociale foerageerstrategie en de noodzaak voor de jongen om relatief vroeg zelfstandig te zijn.- (Eds.)