

POLYGAMY IN THE MARSH HARRIER, *CIRCUS AERUGINOSUS*: INDIVIDUAL VARIATION IN HUNTING PERFORMANCE AND NUMBER OF MATES

by

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(With 17 Figures)
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1. INTRODUCTION

Polygamous relationships have long attracted the interest of evolutionary biologists concerned with mating systems and sexual selection. The theoretical framework adopted to explain the incidence of polygamy associates its occurrence with a disparity between the sex roles in raising the offspring. The customary view is that only the sex which spends little time and effort on the young can afford to mate with more than one partner at the same time (ORIAN, 1969; MAYNARD SMITH, 1977). LACK (1968, p. 162), for instance, concluded that 'Polygyny, promiscuity and polyandry can be evolved only in species in which one parent can raise the family unaided.' TRIVERS (1972) observed that not the parents' effort itself is crucial to understand such mating systems, but the degree to which it reduces the probability of future offspring. He introduced the concept of parental investment, but adhered to the opinion that it is the sex with the smaller parental investment which benefits from mating with two or more partners. In a thoughtful review, EMLEN & ORING (1977) also stated that 'polygamy is more frequent in species where one sex is freed

¹⁾ Piet WILDSCHUT spent the summer of 1978 with us collecting the time budget data of Marsh harriers and contributed significantly to the data on nestling growth and reproductive success. We are deeply indebted to him, as we are to Jitske BRUINENBERG-RINSMA, Hans KRÜSE and Jaap MULDER, for allowing us to use their data on prey deliveries. We thank several officers (Ing. W. DE VRIES, Drs L. ZWARTS) of the Rijksdienst voor de IJsselmeerpolders for technical help with work in the Lauwersmeer. As always, Dick VISSER carefully prepared the figures and Mrs M. J. DAAN-STIEMENS and Mrs H. LOCHORN-HULSEBOS typed various versions of the manuscript. We appreciate critical comments on an earlier version from Dr J. M. TINBERGEN.

from parental care duties', but in addition they stressed the importance of environmental conditions shaping the opportunities for different members of the species to have more than one mate.

This theoretical framework, while conceptually useful, poses a dilemma to the field biologist, since parental investment can not directly be measured. As TRIVERS pointed out, the effort expended on the young, whether expressed in time or energy, is not a reliable guide to parental investment. That he nevertheless continued to interpret incubation shifts and food deliveries in starling parents as evidence for sex differences in parental investment (*loc. cit.* p. 143) underscores the dilemma. It becomes especially troublesome if one considers polygamy in raptorial birds, where the sex mating with several partners, *i.e.* the male, usually provides nearly all of the food for its mates and again most of the food for the nestlings. Either parental investment is not necessarily associated with parental effort or polygyny is not a consequence of small male investment. The situation in raptors apparently requires our attention if we are to understand the evolutionary stability of polygamous mating systems in general. NEWTON (1979, pp. 31-37), carefully reviewing mating systems in raptors, deplored the lack of information on the success of individual birds in relation to their mating status. Needed is an analysis of the costs and benefits to individual birds as associated with their breeding behaviour. Breeding success may be considered as a first approximation of the benefits to birds taking different options. The costs in terms of future offspring can not be directly established. We may, however, compare the efforts expended on the offspring by parents following different strategies, as a step towards an empirical basis of mating system theory.

The present study was aimed at quantifying how parental effort was divided up among the sexes, and distributed over the partners, and which effects this had on the numbers of offspring raised. More specifically, we attempted to obtain complete time budgets for individual marsh harrier (*Circus aeruginosus*) males engaged in mono-, bi- and trigamous relationships, for a significant portion of the breeding season. The analysis of hunting yield and frequency allowed a comparison of the individual quality of parental care. In this analysis, the net hunting yield, *i.e.* the prey returned to a male's nest(s) per hour of foraging is interpreted as a measure of hunting quality. This assumption roots in the now widely accepted view that animals while foraging generally maximize their rate of energy gain (*e.g.*, PYKE & *et al.*, 1977 for review). This remains unproven for parent marsh harriers, and we should be aware that other altricial birds have been shown in response to nestling demands to take foraging

decisions which do not maximize capture rate but probably enhance fitness otherwise, *e.g.* by improving nutrient balance or safety from predators (TINBERGEN, 1981). In the harriers, where no such field experiments are available, we are restricted to a descriptive analysis, and the data should help in the construction of hypotheses, rather than be viewed as their test. The assay of individual time budgets in raptors is a time consuming enterprise. This obviously restricted our data to only a few individuals. Yet the patterns found are indicative of considerable interindividual variation, both in hunting quality and in parental effort, and allow a fresh look at the theoretical basis of mating systems in raptors.

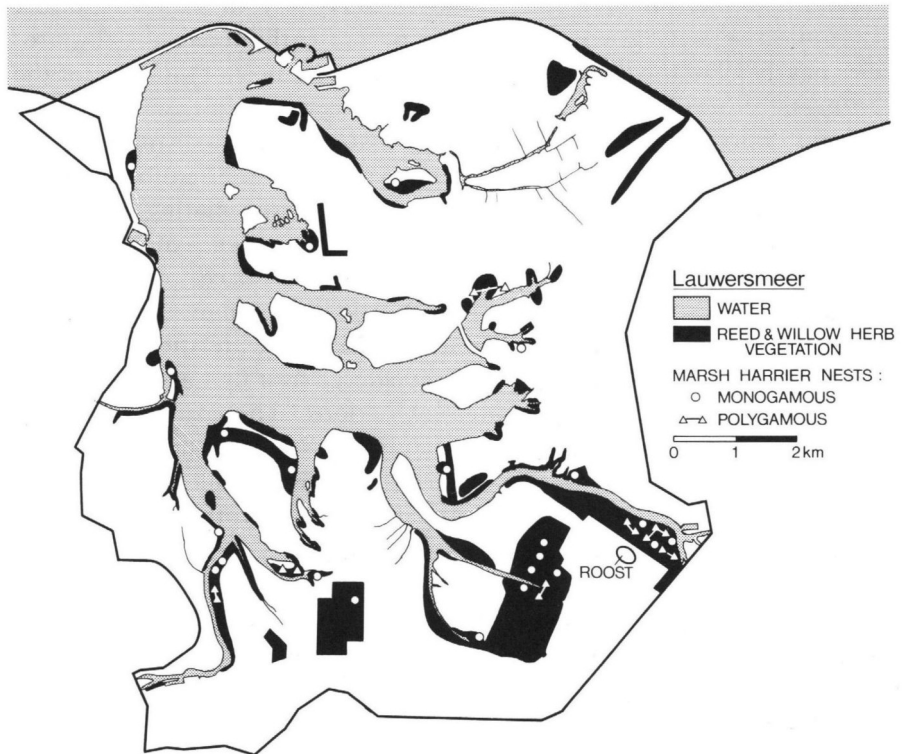


Fig. 1. Map of the Lauwersmeer area showing the extension of reed and willow herb vegetation and the location of marsh harrier nests in 1978.

2. STUDY AREA AND METHODS

The study was carried out in and around the Lauwersmeer (53°20'N, 6°10'E), a newly reclaimed polder in the Netherlands, which largely underwent a natural development since the reclamation in 1969 (Fig. 1; and see JOENJE, 1978). In this area a rapidly growing population of marsh harriers established during the 1970's, such that at the end of this

decade some 40-50 broods were raised annually (WILDSCHUT *et al.*, 1982). During 1977-1980, we determined the incidence of polygamous relationships among all parents by finding the nest sites and by long continuous observations of male parents bringing food to the females and nestlings. Individual identification — necessary to establish polygamy — was possible due to the considerable variation in male plumage and colour pattern. Birds were not tagged for individual recognition. In addition to data on polygamy in the Lauwersmeer population of marsh harriers we make use of data collected in 1976-1980 in the polders of Flevoland. These data concern the occurrence of polygamy and the reproductive success associated with it.

Nest observations to establish prey deliveries to the nestlings were carried out on 26 nests belonging to 16 males (1976: 9 nests in Flevoland, observations by H. KRUSE & J. MULDER; 1977: 11 nests in the Lauwersmeer; observations by J. BRUINENBERG-RINSMA;

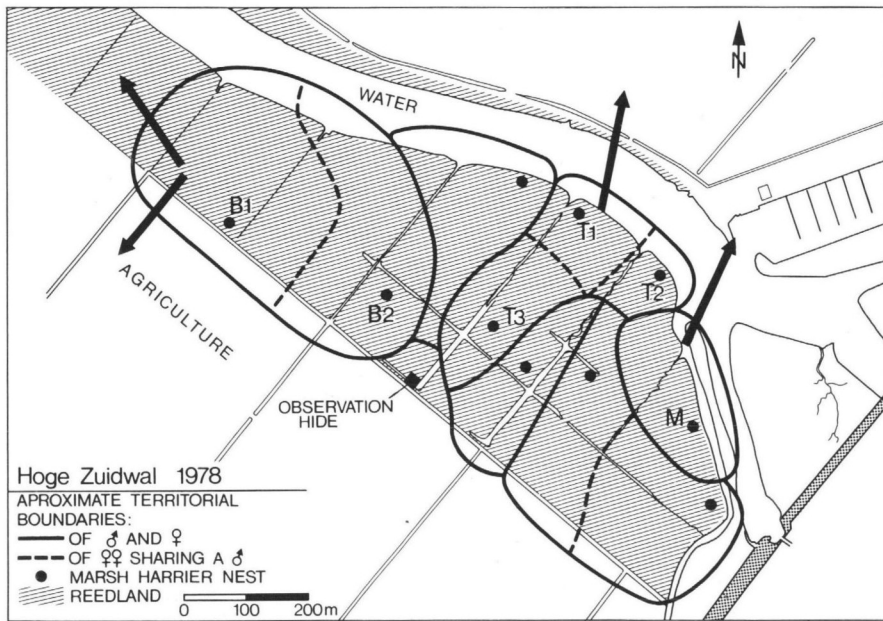


Fig. 2. Location of nests and approximate territorial boundaries of marsh harriers in the 1978 study area. Arrows indicate main flight directions of males leaving on foraging trips.

1978: 6 nests in the Lauwersmeer; observations by W. A., J. S. and P. WILDSCHUT). Phenological data were collected in regular visits to the nests: occasionally in the incubation phase, and every 4 or 5 days in the nestling phase to determine prey remains and growth of the young.

The breeding season as a whole can be subdivided in the following — partly arbitrarily separated — phases.

Courtship (C). This phase lasts from the arrival in the breeding area until the first egg is laid, and includes territorial establishment. The phase lasts about 2-3 weeks.

Incubation (I). This phase (*ca* 33 days) includes the laying period, since incubation generally starts with the first egg.

Nestling phase (N). This phase was defined as beginning with hatching of the first egg till 28 days after hatching of the last egg. During this time the young typically stay in the nest, either continuously or at least at night; they are fed in the nest.

Straggling phase (S). The episode between 28 and 45 days after hatching of the last egg. In this phase the young birds usually stay away from the nest but do not yet fly spontaneously and are fed on temporary nest sites by the parents.

Fledging phase (F). Days 45-73. The young fly around but still receive food from the parents, either on the ground or in the air.

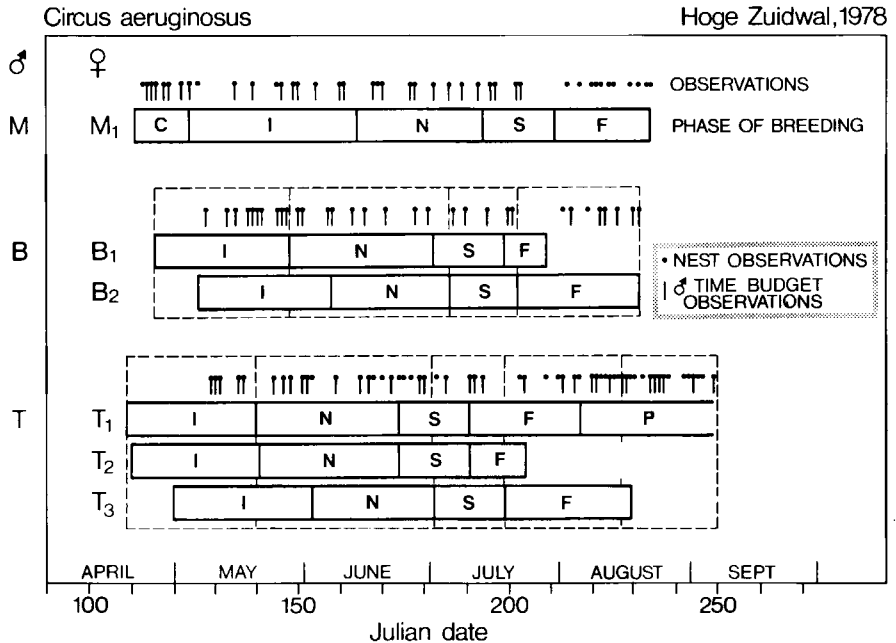


Fig. 3. Phenology of breeding in the six nests studied intensively in 1978 and dates of observations on the three males (M, B, T) and their females (M1, B1, B2, T1, T2, T3). Phases of the breeding cycle are indicated as follows: C = courtship, I = incubation, N = nestling phase, S = straggling phase, F = fledging phase, P = Post breeding.

Postbreeding (P). From day 73 onwards the young are grown-up, receive food only occasionally. Our observations concern only the first 20 days of this phase.

In 1978, an intensive behavioural study was carried out on the parents from six nests throughout these phases of the breeding season (Fig. 3). We attempted to establish time budgets for the parents in addition to their prey deliveries to the nest in order to obtain information on their hunting performance. These nests were situated close together on the 'Hoge Zuidwal', an area of 50 hectares of ruderal land (Fig. 1, 2). This habitat has a vegetation dominated southwards from the waterbank in sequence by reeds (*Phragmites australis*), fiorin (*Agrostis stolonifera*) and willow herbs (*Epilobium hirsutum* and *Chamaenerion augustifolia*). The area was inhabited by six males and ten females. Each male defended an exclusive breeding territory against rivals. Females likewise had exclusive breeding territories. Two males and their territories were shared each by two females,

who in turn defended their own breeding ground against their rivals. One male was trigamous: its territory accommodated three different females and their nests (Fig. 2).

On the edge of the reedland we mounted an observation hide on a tower 4 metres above the ground, at the start of the 1978 breeding season. From this hide, watches were kept throughout the summer and food deliveries at the various nests observed. We kept record of the numbers of prey brought by both parents, and estimated prey species and sizes in four size categories.

In addition, we attempted to obtain time budgets as complete as possible for the three individual males — one trigamous (T), one bigamous (B) and one monogamous (M). As the hunting grounds extended far outside the breeding territories (Fig. 9), this required the help of an observer following the hunting birds by car. Observers in the hide and in the car stayed in contact by hand-held radios. Observations were all done with binoculars (7 × 50) and telescopes (15–60 ×). The time budgets were established by recording every minute the behaviour the bird was engaged in. The following behavioural categories were used:

Flying: Foraging: Hunting: slow and curved flight, often gliding, usually less than 5 meters high.

Directional flight: flights to and from the hunting grounds; transportation of prey; commonly above 5 meters.

Non-foraging: Territorial behaviour: chasing intruders of both sexes, sometimes also crows, magpies, buzzards and kestrels.

Courtship flight: for description see GLUTZ VON BLOTZHEIM *et al.* (1971) and CRAMP & SIMMONS (1980).

Nestbuilding: transport of nest material (twigs, reeds, *etc.*).

Sitting: Perching: in small trees, on mounds *etc.*

Sitting on the ground: In both positions, resting or preening occurred. We actually lumped all sitting behaviour. There has never been any indication of hunting from perches or in other sitting positions. For a detailed description of the hunting behaviour we refer to SCHIPPER *et al.* (1975) and SCHIPPER (1977).

Onset and end of the daily activity could be easily recorded since the male harriers assembled loosely in a nocturnal roost ca 500 meters away from the breeding territories (see Fig. 1) throughout the season. Their departure and arrival times in the roost were considered to delimit the daily activity time. In addition to the time budget data, records were kept of spatial movements as closely as possible. Of course observations by single observers without triangulation can not reveal precise locations. We have therefore not aimed at detailed movement analyses as were attempted on the basis of distant observations of hen harriers by SCHIPPER (1977). However, since we followed the birds by car, observations were usually close enough to obtain reliable home range estimates.

The observation dates for each of the three males and their nests are indicated in Fig. 3. The majority of the data was collected in units of about nine hours: half days, either from sunrise till noon, or from noon till sunset. Occasionally, observations were made from sunrise till sunset continuously (see Fig. 5).

3. PARENTAL PLANNING: THE NUMBERS OF MATES AND EGGS

While polygamy occurs also in other raptors, although infrequently (NEWTON, 1979), it is found rather regularly among harriers (SCHIPPER, 1977). Polygamous pairbonds have been studied in detail in hen harriers (*Circus cyaneus*; PICOZZI, 1978; BALFOUR & CADBURY, 1979). In the marsh harrier, clear evidence on the occurrence of polygamy has been provided

by SCHIPPER (1977), who found a ratio of 20:19 nest of polygamous versus monogamous males in the Netherlands. Incidental observations of polygamous males were reported by HOSKING (1943) in South England, HILDÉN & KALINAINEN (1966) in Finland, BENGTSON (1967) in South Sweden, SACH (1967) on the isle of Sylt, and THIOLLAY (1970) in the Camargue. For other cases see CRAMP & SIMMONS (1980). There is little evidence available on the frequency of occurrence of polygamous relationships or on their phenomenology: environmental conditions, clutch sizes and laying dates. It seems useful therefore to begin with a documentation of the phenomenon, based on the situations in Flevoland and the Lauwersmeer, where polygamy has been observed regularly since 1976.

Environmental conditions generally considered conducive to the occurrence of polygamy are characterized by:

- a) temporal abundance and spatial heterogeneity of food sources (VERNER & WILSON, 1966);
- b) restricted nesting grounds and vast feeding areas (CROOK, 1965; ORIANS, 1969; VON HAARTMAN, 1969);
- c) early stages of succession (ORIANS, 1969).

Both the Lauwersmeer and the area where marsh harriers breed in Flevoland are recent land reclamations and can be considered as early stages in ecological succession. In the Lauwersmeer nests of marsh harriers were found nearly exclusively in the dense vegetation of reeds and willow herbs along the banks of the lake and creeks (Fig. 1). The hunting grounds of the harriers stretched out far over the surrounding arable land (Fig. 9). Thus, both characteristics b) and c) seem to apply to the marsh harrier polygamy situation in the Lauwersmeer. In Flevoland, polygamy was frequent also in extensive breeding areas and restriction of such areas seems not to be a necessary condition therefore. We have made no attempts to quantify the very diverse food sources of the harrier in the area. Hence no conclusions can be drawn of food patterns and processes in relation to the incidence of polygamy.

In order to analyse differences in clutch size and laying date in relation to polygamy, we first discuss the interrelationship of these parameters. Laying dates of the first egg of each clutch were calculated from regular (*ca* fortnightly) nest visits using the following approximate assumptions: (SCHIPPER, 1973; GLUTZ VON BLOTZHEIM, 1971; BOCK, 1979): 1) eggs are laid in 2-day intervals; 2) incubation lasts 33 days; 3) growth of the young follows the general curves for ♂♂ and ♀♀ given by WILDSCHUT *et al.* (1982). It is estimated that laying dates based on these calculations will be correct to within 2 days when based on clutches found incomplete during

TABLE 1
Annual mean laying dates and clutch sizes in marsh harriers in relation to mating status

Laying date	Flevoland (52°25' N 5°30' E)				Lauwersmeer (53°20' N 6°10' E)				(n)		
	1976	1977	1978	1979	1980	mean ± sd	1977	1978		1979	1980
Monogamy	117	114	119	116	113	114 ± 11	123	121	121	118	121 ± 10
Bigamy: ♀ 1	108	107	—	115	105	107 ± 5	116	115	116	118	115 ± 5
♀ 2	120	114	—	123	114	116 ± 5	128	127	129	122	128 ± 10
All birds	117	113	117	118	112	114 ± 12	117	121	122	117	120 ± 10
Clutch size											
Monogamy	5.2	5.0	4.9	4.7	5.2	5.0 ± 1.1	4.6	4.3	4.5	5.2	4.7 ± 1.0
Bigamy: ♀ 1	4.6	4.5	—	5.0	5.6	5.1 ± 1.1	4.8	4.5	4.5	5.0	4.5 ± 0.9
♀ 2	4.7	5.5	—	4.0	5.8	5.2 ± 0.9	5.5	3.8	5.0	4.0	4.6 ± 1.1
All birds	4.7	4.1	4.7	4.6	5.5	4.8 ± 1.0	4.8	4.2	4.7	5.1	4.9 ± 1.0

Laying dates of the first egg are given as Julian dates (*e.g.* 100 = 10 April).

laying and to within 4 days when based on size of recently hatched nestlings. Mean annual laying dates (Table 1) for all clutches ranged from Julian dates 111 (22 April) to 118 (28 April) in Flevoland and from 116 (27 April) to 122 (2 May) in the Lauwersmeer. Thus annual differences were small compared to interindividual variation (overall standard deviations of 12 and 10 days, respectively). There was a consistent difference between the two study areas. Marsh harriers in Flevoland bred on average ca 6 days earlier (t-test; $p < 0.005$) than in the Lauwersmeer (Table 1).

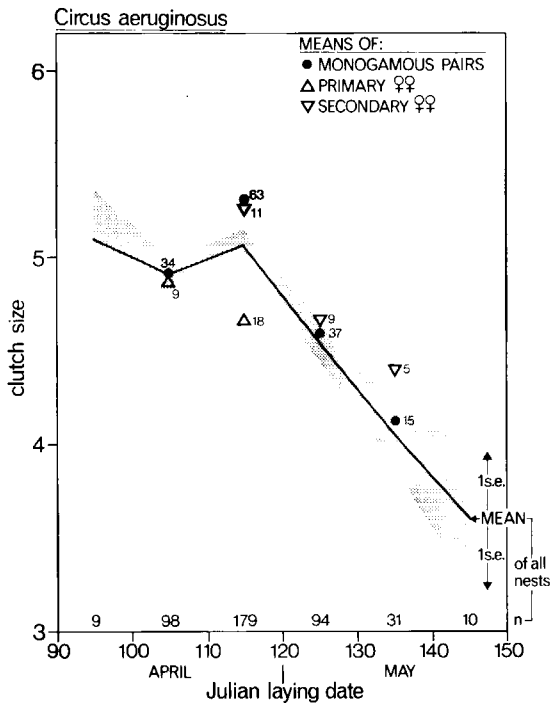


Fig. 4. Clutch size as a function of laying date of the first egg for monogamous pairs and for the primary and secondary females in polygamous pairbonds.

In both areas a similar relationship between clutch size and laying date was found, as documented extensively by WILDSCHUT *et al.* (1982). Clutches started later were generally smaller than clutches laid early in the year. The marsh harriers in this respect followed a common pattern in the breeding behaviour of raptors (*e.g.* NEWTON, 1979; CAVÉ, 1968; DIJKSTRA *et al.*, 1982) as well as of many other birds (*e.g.*, PERRINS, 1970;

KLOMP, 1970; DRENT & DAAN, 1980). No systematic differences existed between the sizes of clutches started at any given date in Flevoland and the Lauwersmeer (WILDSCHUT *et al.*, 1982). We have therefore pooled all available data on 421 nests. Fig. 4 summarizes the general decrease in the average size of clutches laid from day 120 (April 30) onwards. Of these 421 clutches, 157 were known to be laid by females in monogamous pairbonds. Their clutches closely match the curve obtained for all nests. 59 females were known to be engaged in polygynous bonds. Among these, we distinguish between primary and secondary females of a bigamous male, on the basis of their date of laying. On average, such females involved in polygamous bonds differed neither in laying date nor clutch size from monogamous pairs (Table 1). However, the primary female on average was significantly ahead of the monogamous pairs (7 days in Flevoland, t -test $p < 0.01$; and 6 days in the Lauwersmeer, $p < 0.001$). The secondary female laid her eggs on average slightly later than the females of monogamous pairbonds (Flevoland: difference of 2 days, not significant; Lauwersmeer: 7 days, $p < 0.001$). Yet, clutch sizes were virtually equal for monogamous females and for primary and secondary females of a bigamous male (Table 1). This would imply that primary females laid clutches slightly smaller than predicted on the basis of laying date, while the clutches of secondary females were slightly larger than predicted. Indeed in all groups of laying dates secondary females had clutches larger than the average female (Fig. 4), although in none of the intervals the material is large enough for statistical significance. Primary females on the other hand, had smaller clutches than average, at least in the interval day 111-120 (April 21-30), where the gradual decay in clutch size starts (Fig. 4). Clutches started in this interval, where also the largest samples were available, contained on average 0.6 eggs more when laid by secondary than when laid by primary females. The difference is statistically almost significant ($p < 0.1$, one-tailed t -test), and seems to deserve our understanding as a non-trivial aspect of polygamous strategies. We shall raise some speculations about it in section 6.5.

4. PARENTAL EFFORT: TIME BUDGET AND FORAGING RETURN

4.1. The male's effort.

In marsh harriers, like in many other raptors, it is the male who provides food for the female(s) during incubation and who also has a major share in the prey deliveries to the young. We have not attempted to quan-

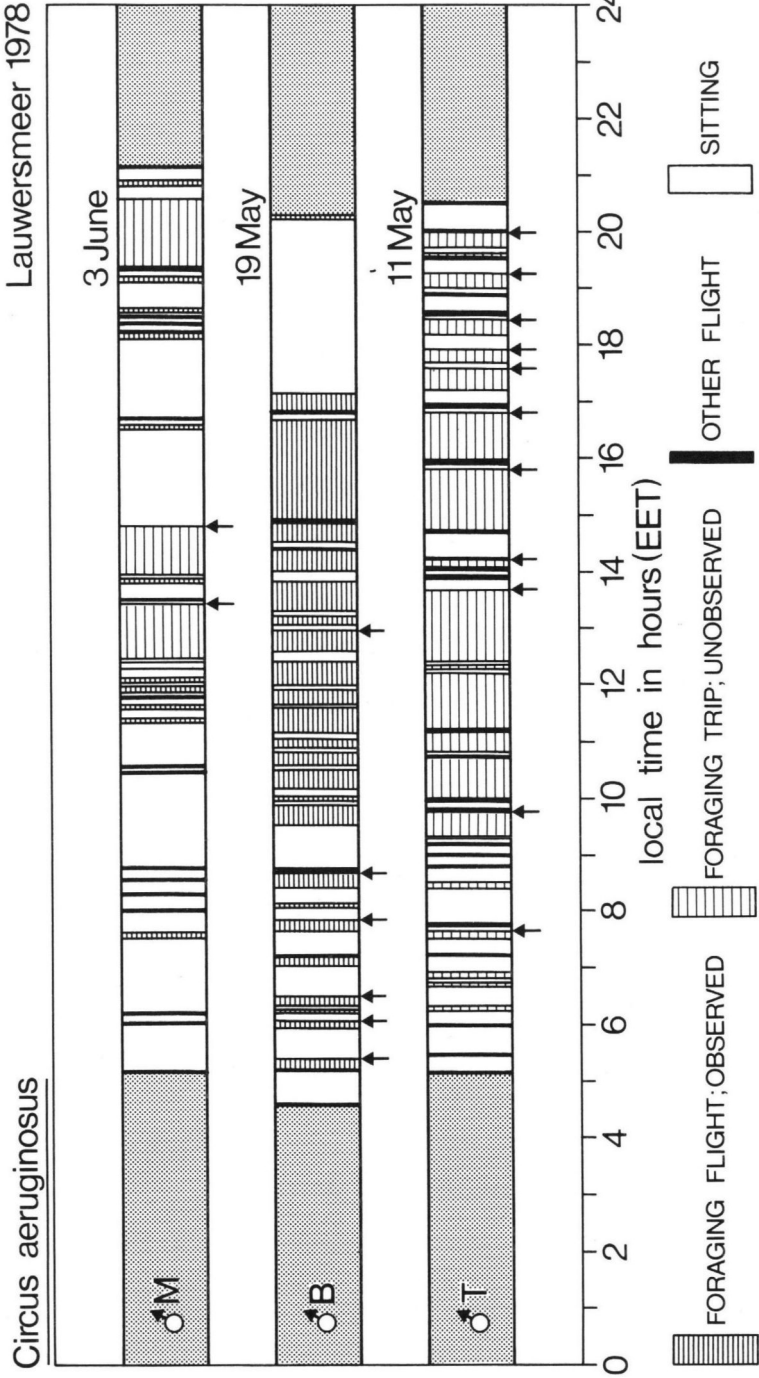


Fig. 5. Examples of behaviour protocols taken from three males during the incubation phase. Males M and T were not continuously observed during their foraging trips on these days. Observations on other days indicated 60% flying during foraging trips.

tify the energy spent by the males in obtaining this food, but we analyse how much foraging time was needed in relation to the number of nests attended.

Fig. 5 shows by way of example the results of three complete days of observations in the incubation phase on the basis of the behavioural categories described (most of the data were collected in half day units). In these three examples, only male B was continuously followed on its foraging flights outside the breeding territory. A large number of such half and whole observation days (Fig. 3) have been the starting point for the present analysis.

4.1.1. *Time budget.*

To compare data collected in various phases of the breeding season, we have to take the changing daylength into account. As a diurnal bird the marsh harrier extends its active day with the lengthening days in summer

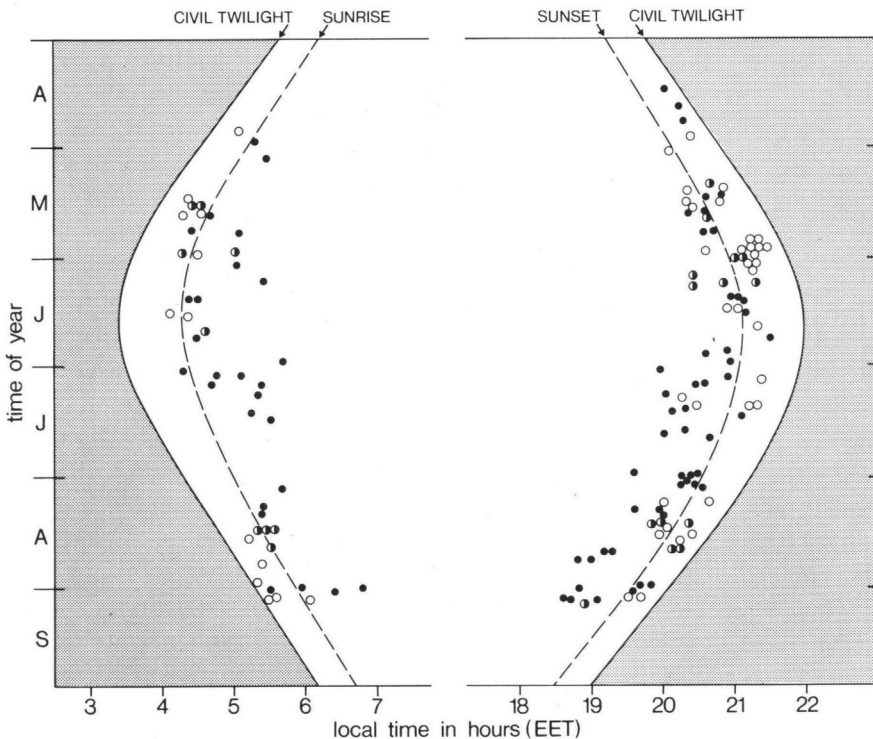


Fig. 6. Times of departure from and return to the night roost in three marsh harrier males during the breeding season. Symbols indicate degrees of overcast: \circ clear (0-2/8 cloud cover); \odot partly clouded (3-5/8); \bullet heavy overcast (6-8/8).

(Fig. 6). As in many other bird species (ASCHOFF & WEVER, 1962) the daily onset and end of activity in marsh harriers are subject to influences of light intensity. We distinguished days with clear sky, medium or heavy overcast. On clear days activity started significantly earlier and ended significantly later than on heavy overcast days. This is true whether onset and end are tested with respect to civil twilight (two-tailed Wilcoxon test, $p < 0.025$ and $p < 0.025$, respectively) or with respect to sunrise and sunset ($p < 0.005$ and $p < 0.025$ respectively). Bright weather slightly lengthens the active day, cloudy weather shortens it. In this reaction to light intensity there were no distinct differences between the males, so that average active day length was similar for them in the different reproduction phases (Fig. 10).

With the breeding season in progress a number of things were changing for all three males in a corresponding way. In the first place they shifted their activities in the course of the season, especially after the incubation phase, away from the breeding territory to what we have called the hunting-ground (Fig. 7). Together with this spatial shift, the average duration of the foraging flights outside the breeding territory increased strongly (Fig. 8). Simultaneously, the variation around this average increased. This shift was further accompanied by extension of the total home range (Fig. 9). The sizes of the home ranges of the monogamous and trigamous male during the nestling, straggling and fledgling phase were considerably larger than those mentioned by other authors (Table 2). It is possible that at least a part of this deviation can be accounted for by differences in intensity of observation. The statement by SCHOENER (1968) that home range size increases with decreasing prey density can not be verified here due to lack of data. In breeding bird censuses (P. ESSELINK, p.c.), there was some suggestion that the home range of the bigamous male may have been richer in prey (especially breeding waders) than that of the two other males, although we did not quantify prey availability. It should further be noted that the male's hunting ranges had a large measure of overlap. Other males were making use of the same hunting grounds.

The decreasing time spent daily by the males in the breeding territory, the increasing duration of the foraging flights and the extension of the home range, are all connected with a fundamental change of behaviour during the different phases. There was a general increase in the total daily foraging activity in the course of the season (Fig. 10). Foraging activity had a maximum (of nearly 8 hours) during the nestling and straggling phases and decreased again in the fledgling phase. Minimal foraging ac-

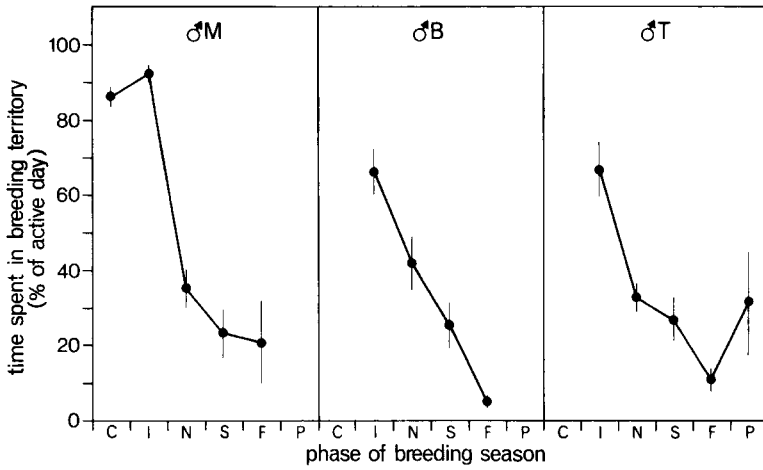


Fig. 7. Time spent in the breeding territory by three marsh harrier males in the course of the breeding season. Means \pm 1 standard error.

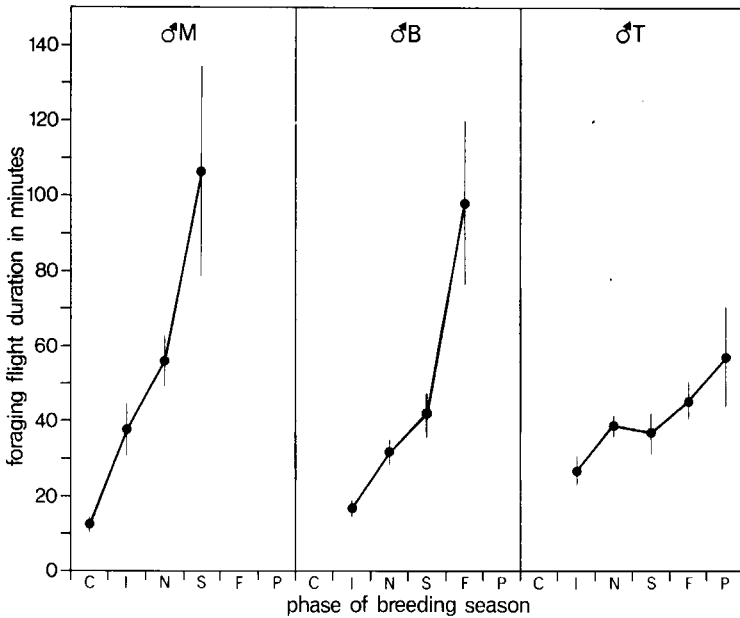


Fig. 8. Durations of foraging flights away from the breeding territory in three marsh harrier males in the course of the breeding season. Means \pm 1 standard error.

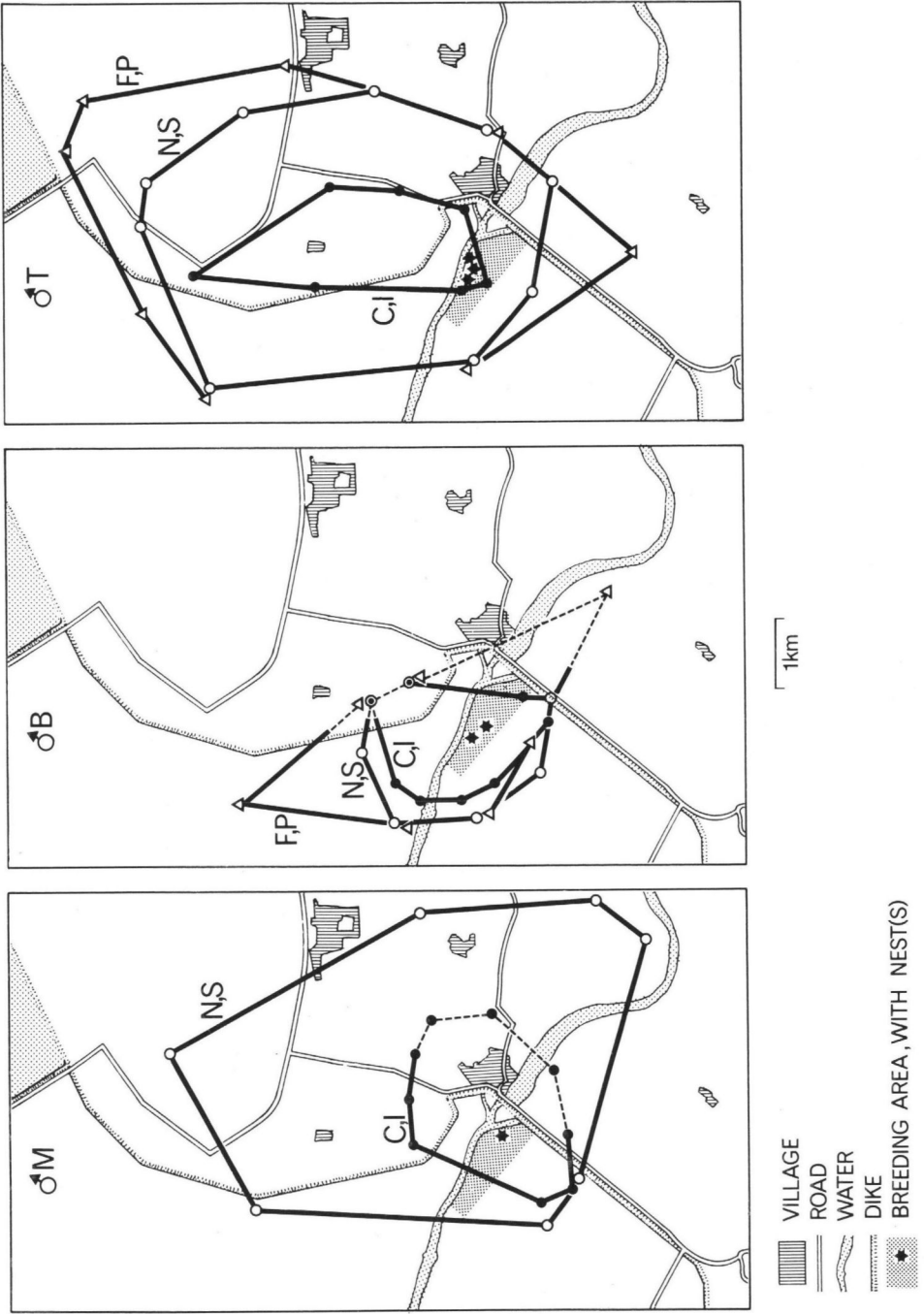


Fig. 9. Convex polygon hunting ranges of three marsh harrier males during different parts of the breeding season: CI = courtship + incubation phases; NS = nesting + straggling phases; FP = fledgling + post fledgling phases.

tivity occurred in the incubation phase and after the breeding season (ca 30%). A similar seasonal cycle was found in the white-tailed kite, *Elanus leucurus* (WARNER & RUDD, 1975).

These seasonal changes in total daily foraging activity were accompanied by marked changes in its daily distribution (Fig. 11). At the seasonal peak in foraging activity coinciding with the nestling and straggling phase, foraging was about equally distributed throughout the day (ca 50% of time). When total activity was lower, maxima of 40-50% occurred only during a daily foraging peak around noon. We suggest that values around 50% of the time spent in foraging may represent an upper limit and that increased demands during the nestling and straggling phases are met by increased activity at times of day (early morning and late afternoon) while this limit is not reached in other breeding phases.

TABLE 2

Sizes of convex polygon home ranges (in hectares) of male marsh harriers during the breeding season. For comparison, home range data from other studies are included

Study area	Home range			Source
	M	B	T	
Lauwersmeer (Neth.)				
C, I phase	440	310	410	
N, S phase	2360	420	1970	
F, P phase	-	730	2610	
Camargue (Fr.)		270 -	420	THIOLLAY (1970)
Flevoland (Neth.)		250		SCHIPPER (1977)
Groote Peel (Neth.)		390 -	500	SCHIPPER (1977)

Fig. 10 indicates for our three harrier males the number of hours spent foraging per day as well as the length of the active day. The large foraging activity in the courtship phase of the monogamous male (the only one of the three males that was observed during courtship) is probably more general. Observations on another bigamous male in the same phase of reproduction showed corresponding results. The differences between the males in foraging activity in the successive phases are generally small. Both polygamous males foraged a little longer per day, although this was not statistically significant (only B *versus* M in the incubation phase (one-tailed Wilcoxon test, $p < 0.05$)). However, the total foraging time accumulated over the whole breeding season (from the start of the incubation phase till the end of the fledgling phase) is strikingly different. Together with the number of females the duration of the breeding care of

the male increases and with that the total time spent on foraging activity (Table 3).

4.1.2. Foraging return.

As in foraging activity, there was a clear seasonal cycle in the total numbers of prey returned to the nest per day by our three males, again with a maximum in the nestling and straggling phases. In all except the

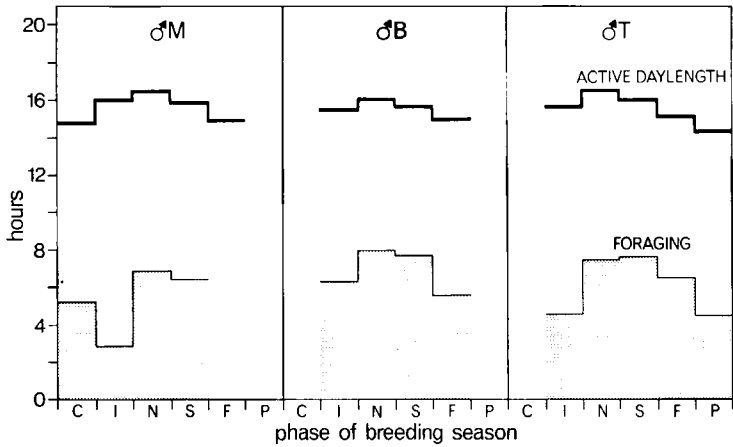


Fig. 10. Length of the active day and the time spent foraging per day by three marsh harrier males in the course of the breeding season.

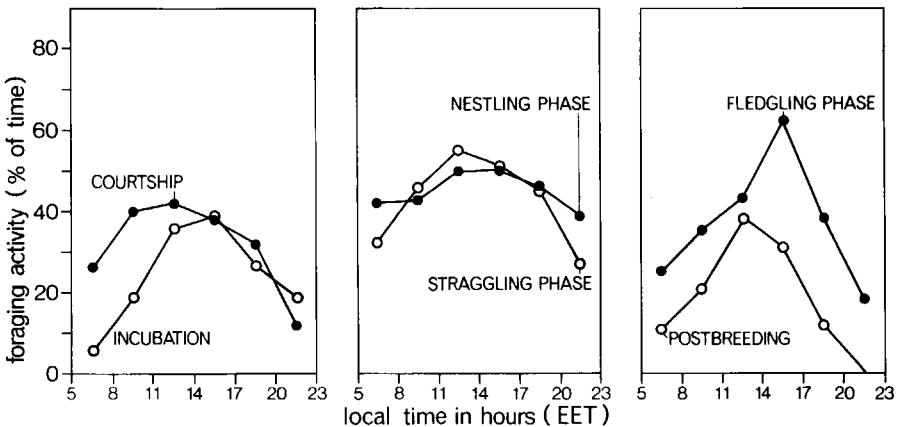


Fig. 11. Daily rhythm in foraging activity in three marsh harrier males in different phases of the breeding season: Average percentages of time spent foraging per 3-hr block of the day.

fledgling phase the polygamous males brought more prey than the monogamous male (Table 4). In the fledgling phase, when prey deliveries of the males M and B dropped rapidly, the number of prey returned by the trigamous male exceeded that of the other two. Two earlier series of observations, by J. KRÜSE & J. MULDER in Flevoland in 1976, and by J. BRUINENBERG-RINSMA in the Lauwersmeer in 1977,

TABLE 3

Total parental effort involved in raising the young of six nests, from the beginning of incubation till the end of fledging

Bird	Males			Primary females				Secondary females	
	M	B	T	M1	B1	T1	T2	B2	T3
Length of period of prey deliveries to the young	108	112	121	45	60	40	55	60	70 days
Age of oldest young at start of female foraging	—	—	—	22	9	16	13	2	3 days
Estimated total foraging time	534*	782	762	—	—	—	—	—	— hours
Total number of prey brought	500	1250	1365	150	230	160	180	220	430 prey
Average prey size category	1.6	1.7	1.9	1.6	1.9	2.0	2.0	1.7	1.7 —

Estimations based on extrapolation from the half-days of observation. * = Figure perhaps slightly overestimated since incomplete time budget data for the nestling phase were replaced by straggling phase data.

TABLE 4

Total foraging return by three marsh harrier males

Male	M			B			T								
	n	pd	sc	n	pd	sc	n	pd	sc						
Phase of breeding season	C	9	2.1	—	—	—	—	—	—						
	I	12	2.2	1.3	31	6.3	1.5	24	8.8	2.1					
	N	47	8.6	1.7	93	13.8	1.9	129	12.7	2.0					
	S	7	3.3	1.5	73	17.9	1.5	41	13.4	2.1					
	F	31	5.3	1.5	25	5.9	1.6	96	11.4	1.7					
P	—	—	—	—	—	—	25	4.1	1.7						
Prey size category	I	II	III	IV	I	II	III	IV	I	II	III	IV			
Number of prey (whole season)	47	41	6	1	1.6	109	73	32	2	1.7	104	130	58	5	1.9

n = number of prey observed; pd = prey deliveries per day; sc = average size category (not indicated when less than 5 prey classified).

revealed similar differences. Fig. 12 combines all nest observations available for males with one, two and three females, and demonstrates both the seasonal trend in foraging return and the dependence on nesting status. In addition to bringing most prey in any phase of the breeding cycle, the trigamous male had a longer extension of its total annual period of breeding care. Hence the total number of prey delivered annually to females and juveniles was larger in this male than in bigamous or monogamous males (Table 3).

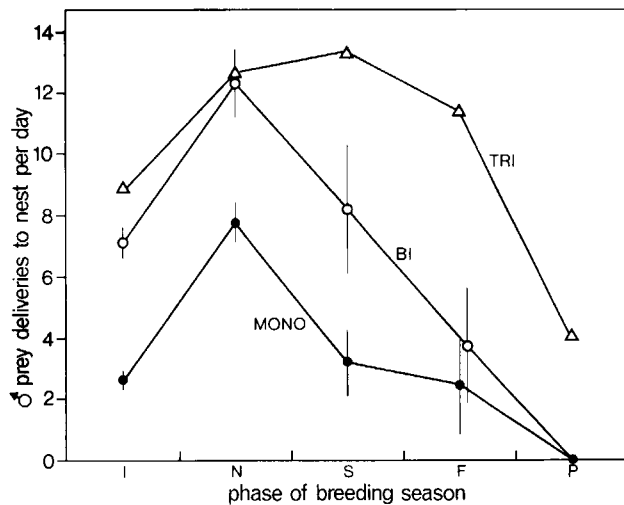


Fig. 12. Foraging return in 5 monogamous, 6 bigamous and 1 trigamous male marsh harrier in the course of the breeding season. Means \pm 1 standard error. Based on nest observations by J. Bruinenberg-Rinsma, H. Krüse and J. Mulder and this study.

The number of prey brought to the nest certainly does not sensitively reflect the total prey mass or energy delivered. The polygamous males may have brought smaller prey items than the monogamous one, and have compensated this by delivering more frequently. We are not in a position to quantify prey size exactly. However, estimated prey size categories and prey remains in the nest provide evidence that prey brought by the polygamous males actually were larger than those of the monogamous male. Among the prey items that were categorized over the whole study period, the average prey size category of the three males belong to different distributions (χ^2 -test. $p < 0.005$; Table 4). This difference was fairly persistent throughout the season (Table 4). The monogamous male had continuously smaller prey than the trigamous

one, while the bigamous male's prey sizes were intermediate. If this is representative for the other males too, Fig. 12 underestimates the differences in prey biomass returned by males with different mating status.

4.1.3. *Hunting yield.*

The combination of foraging activity and foraging return gives us the number of prey brought per hour of hunting. We call this the *net hunting yield*, since it does not include the prey items eaten by the bird itself on its foraging trips. Again, there is a seasonal cycle with a maximum in the nestling and straggling phases (Fig. 13). The differences between the males are striking. In each phase the polygamous males differ significantly (Wilcoxon test, one-tailed $p < 0.05$) from the monogamous male (except M versus B in the nestling phase, $p < 0.1$), in spite of the small number of

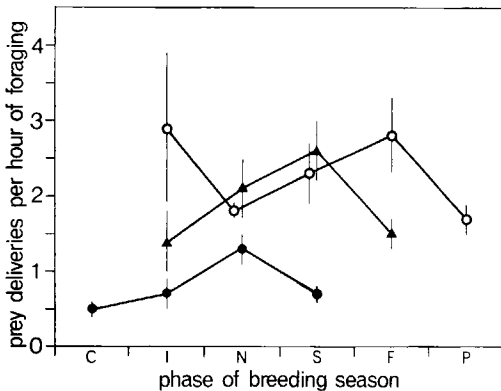


Fig. 13. Net hunting yield in three marsh harrier males in the course of the breeding season. Means \pm 1 standard error.

observation days and of the variation between such days (as related for instance to weather conditions). Net hunting yield of the monogamous male was consistently lower than that of the polygamous males. Moreover, the net hunting yield of the trigamous males was significantly larger than that of the bigamous male in the incubation and fledgling phase. In view of the differences in average prey size category this again underestimates the interindividual variations in prey weights brought per hour of foraging.

Thus, our three males were clearly distinguished in such a way that the male with the largest net hunting yield had most females, the male with the smallest yield had only one female. Since the trigamous male did not

spend less time foraging than the others, but brought larger prey, the total foraging return to the nests was clearly positively correlated with the number of females.

4.1.4. *Distribution of prey over the nests.*

In this section we discuss how the males divided the prey among their two or three females. In the exceptional case of trigamy the first female (T1) started laying only one day before the next (T2, see Table 8), and both were considered primary females, the third female is treated as a secondary female. Polygamous males did not distribute their prey evenly over the nests (Table 5). During the nestling and straggling phases, when demands were highest, the primary nests received more prey than the secondary nests. The total number of prey brought to the nest from hatching of the first egg till the fledglings were independent was also clearly different: in this study the nests of primary females received *ca* 480 prey, secondary females *ca* 360.

TABLE 5

Prey deliveries per day to the different nests by two polygamous males

Male		B		T		
Female		B1	B2	T1	T2	T3
Phase of breeding season	I	2.8	3.2	1.5	2.6	4.4
	N	8.2	5.6	5.7	4.8	2.0
	S	13.2	4.7	7.2	1.3	4.9
	F	0.0	5.9	5.5	0.0	5.7
	P	—	—	3.8	0.0	0.3

Phase of breeding season correspond with the division for males as in Fig. 3.

The monogamous female was estimated to have received 410 prey, Pooling the data obtained in 26 series of nest observations, we find, however, that polygamous males on average brought to their primary nests as many prey per day as monogamous males brought to their single nests. In Fig. 14, the prey deliveries per day during the various phases of the breeding season are plotted against time of year. The curves describing prey deliveries to primary and secondary nests are slightly displaced relative to each other due to the differences in the dates of initiation of each clutch. In all phases except the fledgling phase, a clear predominance of prey deliveries to the primary nest appears, which is not due to this difference in timing.

The preference of the polygamous males for their primary females was possibly associated with the position of their nests. The preference nests were lying at the beginning (and end) of the hunting flight routes taken (arrows in Fig. 2). Presumably the male responds to the female and young begging for food on it's way home, so that the position of the nests relative to the usual flight route may be of decisive significance.

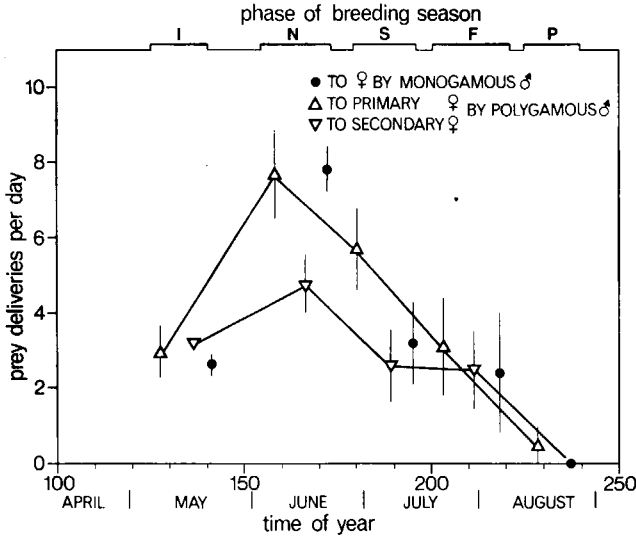


Fig. 14. Distribution of prey deliveries by polygamous marsh harrier males to their primary and secondary females. Means \pm 1 standard error. Observations on 7 polygamous and 5 monogamous males by J. Bruinenberg-Rinsma, H. Krüse, J. Mulder and this study.

4.2. The female's efforts.

No attempt was made to obtain complete time budgets of the females, but data collected on foraging return allow some quantification of the females' efforts. In the polygamous groups, secondary females started to hunt for the young at an earlier age of the nestlings than primary females, and therefore spent altogether more days providing food for them (Table 3). The primary female's total period of hunting for the young seemed to correspond more closely to that of the monogamy-female, than to that of the secondary females. Female effort in collecting food for the young is most pronounced during the straggling phase. It is especially during this phase that the secondary females brought more prey per day than other females (Fig. 15). Prey size categories were similar for the six females,

although slightly larger prey were brought by the primary females B1, T1 and T2 than by secondary females (χ^2 -test, $p < 0.05$, Table 6, prey size categories III and IV pooled).

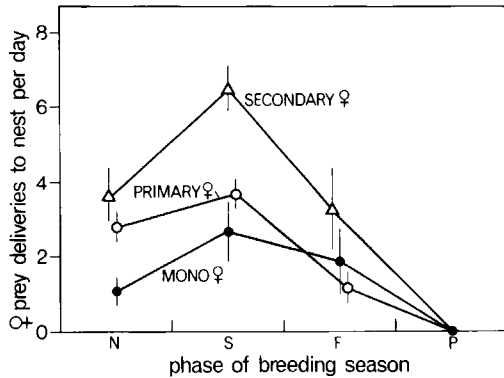


Fig. 15. Foraging return by 9 primary and 8 secondary female marsh harriers and 5 females of monogamous males in the course of the breeding season. Means \pm 1 standard error. Observations by J. Bruinenberg-Rinsma, H. Krüse, J. Mulder and this study.

5. PARENTAL SUCCESS: THE NUMBERS OF OFFSPRING FLEDGED

In evaluating the benefits accruing to parents in monogamous or polygamous relationships our concern should be with total reproductive output into the next breeding generation. This is affected by the chances for survival till the next breeding season both of the parents themselves and of the eggs laid. As in so many studies, only the survival rates for the young until fledgling could be established. These reveal quite distinct patterns, however.

In monogamous nests, three young were fledged on average (Table 7). In the nests of bigamous males about the same number of fledglings were raised, so that these males doubled their reproductive output by taking on an additional female. However, there was a consistent difference between the numbers of fledglings from primary and secondary nests. The primary females raised significantly more young than females with monogamous males, and the secondary females raised significantly less young (Table 7). The difference between primary and secondary females was significantly different from zero only in 19 cases of bigamy in the Lauwersmeer area, but not in Flevoland, where only 11 cases could be

TABLE 6
Total foraging return by 6 marsh harrier females

Female	M1		B1		B2		T1		T2		T3	
	n	sc	n	pd	n	pd	n	pd	n	pd	n	pd
Phase of breeding season	3	0.5	19	2.9	16	2.7	16	2.1	38	3.9	54	7.0
N	8	3.8	19	4.8	21	6.3	12	3.8	6	2.8	14	6.7
S	21	3.6	2	1.0	5	1.1	3	0.4	3	0.4	29	4.9
F	—	—	—	—	—	—	—	—	—	—	—	—
P	—	—	—	—	—	—	—	—	—	—	—	—
Prey size category	I	II	III	IV	I	II	III	IV	I	II	III	IV
Number of prey (whole season)	13	12	1	1	13	16	6	2	17	15	5	0
Average sc	1.6	1.9	1.9	1.7	1.7	2.0	2.0	2.0	2.0	2.0	1.7	1.7

n = number of prey observed; pd = prey deliveries to the nest per day; sc = average prey size category (not indicated when less than 5 prey classified). χ^2 -test of significance of the difference between distributions between primary females (B1, T1, T2: I, 33; II, 49; III/IV, 27 and of secondary females B2, T3: I, 60; II, 50; III/IV, 22; $\chi^2 = 6.22$, $P < 0.05$).

studied. In the six nests under intensive observation in 1978 again the primary females scored the largest number of fledglings (Table 8). The trigamous male achieved one of the largest numbers of fledged young (8) observed in any bird per season.

As we saw earlier (Table 1) there were no systematic differences in numbers of eggs between monogamous and primary or secondary clutches. Hence the variation in numbers of young fledged per nest was due entirely to differential mortality of eggs and nestlings. In Flevoland as well as in the Lauwersmeer, primary clutches had slightly higher rates of survival of eggs till hatching and of nestlings hatched till fledging than nests of monogamous pairs (Table 7B). In secondary nests, egg survival was not consistently different from monogamous nests, but a considerable reduction of nestling survival was found in secondary nests in both study areas. These differences led to nearly equal survival rates of eggs sired by polygamous males as of those by monogamous males, whereas the latter did better (81%) than the former (76%) in the nestling phase.

TABLE 7

Breeding success and offspring survival rates in relation to mating status in marsh harriers

A. Mean number of fledglings \pm 1 standard deviations (n). Significance levels of differences according to one-tailed t-test

B. Percentages of eggs surviving till hatching and of nestlings surviving till fledging

Area	Flevoland (1976/80)	Lauwersmeer (1977/80)	Areas combined
A. Number of fledglings:			
a. Monogamous σ , ϕ	3.1 \pm 1.4 (87)	2.9 \pm 1.5 (69)	3.0 \pm 1.4 (156)
b. Primary ϕ	3.7 \pm 1.7 (11)	3.4 \pm 1.1 (19)	3.5 \pm 1.3 (30)
c. Secondary ϕ	2.9 \pm 1.2 (11)	2.0 \pm 1.4 (19)	2.3 \pm 1.4 (30)
d. Bigamous σ	6.4 \pm 2.1 (12)	5.4 \pm 1.9 (19)	5.7 \pm 1.9 (31)
Significance a-b	n.s.	n.s.	p < 0.1
Significance a-c	n.s.	p < 0.025	p < 0.01
Significance b-c	n.s.	p < 0.005	p < 0.025
Significance a-d	p < 0.001	p < 0.001	p < 0.001
B. Egg and nestling survival rates:			
	(Eggs) Hatched Fledged	(Eggs) Hatched Fledged	(Eggs) Hatched Fledged
a. Monogamous σ , ϕ	(262) 85% 83%	(337) 66% 79%	(599) 75% 81%
b. Primary ϕ	(47) 87% 83%	(86) 79% 94%	(133) 82% 90%
c. Secondary ϕ	(56) 73% 71%	(94) 71% 57%	(150) 72% 62%
d. Bigamous σ	(103) 80% 77%	(180) 75% 76%	(283) 77% 76%

Total survival rates of eggs till fledging were thus approximately equal for monogamous males (65%) and polygamous males (62%). Together with the similar clutch sizes, this accounts for the virtual doubling of young raised till fledging, by males engaged in a bigamous relationship (Table 7A).

Since we regularly obtained body weights of the nestlings during their development, it is possible to compare weights of birds which later died in the nest with those surviving. In the few cases available for comparison

TABLE 8

Breeding performance in six intensively studied female marsh harriers in the Lauwersmeer in 1978

Female	Laying date 1st egg	(Julian date)	Clutch size	Nestlings	Fledglings	Fledglings per male
M1	5 May	(126)	6	2	2	2
B1	27 April	(118)	4	4	4	6
B2	6 May	(127)	4	4	2	6
T1	19 April	(160)	5	4	4	
T2	20 April	(111)	4	4	1	8
T3	1 May	(122)	5	5	3	

TABLE 9

Sex ratio of fledgling marsh harriers

	Flevoland		1975/80 (nests)	Lauwersmeer		1976/80 (nests)	% ♂♂	Significance of difference from 50%
	♂	♀		♂	♀			
monogamous pairs	173	120	(93)	123	89	(73)	58.6	p < 0.01
primary nests	23	18	(10)	25	41	(19)	44.9	n.s.
secondary nests	20	12	(10)	16	20	(19)	52.9	n.s.
total nests	509	403	(303)	164	150	(111)	55.0	p < 0.01

body weights of young which died afterwards were consistently below average (Fig. 16A). This suggests that malnutrition may be an important factor in nestling mortality and that at least part of the differences in parental success as related to mating status may be due to the differences in food supply to the nestlings.

Body weights of surviving young increased rapidly between days 5 and 20 after birth and reached plateau values sometimes after day 26, at

levels around 700 grams for females and 540 grams for males. Average nestling weights of female survivors after day 26 were independent of parent mating status. Among male nestlings, body weights were not significantly different between young of monogamous parents and those of primary females in polygamous bonds (Fig. 16B). In contrast, male nestlings of secondary females after age 26 days weighed significantly less than other male nestling of the same age (t-test, $p < 0.001$). Again, this suggests that the nutritional state of the nestlings in secondary nests was inferior to the conditions of those in monogamy- and primary nests. This difference further suggests that the increased mortality among the nestlings of secondary females was all but compensated by better conditional quality of the surviving nestlings. Finally, it is of interest to note that in

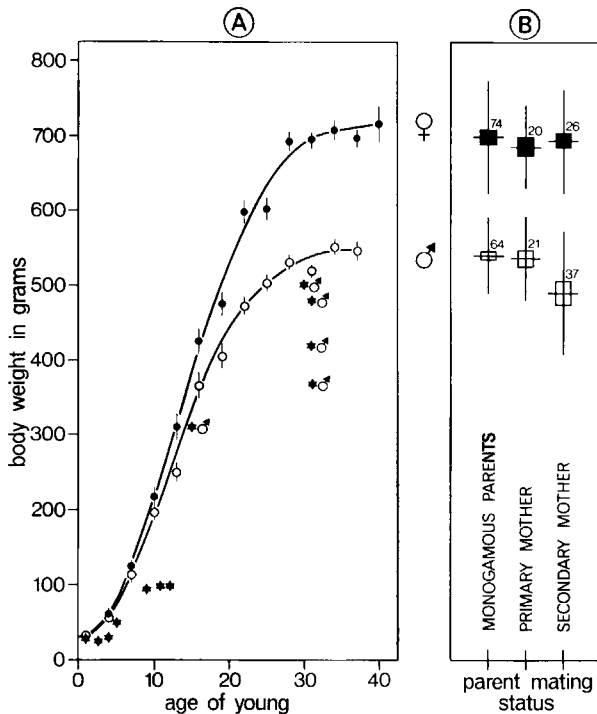


Fig. 16. Body weight of marsh harrier nestlings. A. Average body weights as a function of age (in 3-day age classes, \pm one s.e.m.) in 64 ♀ (●) and 71 ♂ (○) nestlings surviving till fledging. Last live body weights before death are indicated for 14 nestlings not surviving. B. Average body weights (lines: \pm sd; boxes: \pm 1 s.e.m.) of male and female nestlings and 'stragglers' of 25 days and older, for parent with different mating classes. Only male nestlings of secondary mothers were significantly less heavy than other males ($p < 0.01$, Wilcoxon two-sample test).

secondary nests male nestlings died slightly more frequently than females (Fig. 16A) and that only in males a reduced weight after day 26 was evident (Fig. 16B). The male nestlings, which are considerably smaller than the females, may be the first to suffer from a reduced food supply. However, there was no evidence of sex ratios significantly different from 1:1 either in primary or secondary nests (Table 9). When all nests are considered, or only those of monogamous pairs, a sex ratio biased in favour of the males is found.

6. PARENTAL STRATEGIES: HYPOTHETICAL BENEFITS OF POLYGyny

The pressures of natural selection have usually favoured monogamous mating systems in birds (LACK, 1968) and the fact that some female birds choose to mate with males already engaged in an other marital relationship is not readily explained by evolutionary theory. It may, however, be understood on the basis of the 'polygyny threshold model' (VERNER & WILSON, 1966; ORIANS, 1969, 1971). This theory considers the variation in the opportunities for breeding offered by different males. It may be beneficial for females, in terms of the expected number of offspring, to share the good breeding situation of a single male, instead of mating with males with marginal breeding situations. The degree of environmental heterogeneity is instrumental in creating such differences among males, and thereby leading to the occurrence of polygyny as pointed out by EMLEN & ORING (1977). The theory predicts that the relative fitness of females opting for polygynous mating is actually not less than that of females choosing for monogamous relationships.

Empirical analysis of the polygyny threshold theory has largely been based on the breeding successes of females with different mating status. The number of young raised till independence is taken as a measure of their relative fitness (ORIANS, 1969; WITTENBERGER, 1979). Such empirical evidence was derived from field studies mainly on territorial songbirds. The general outcome of such studies is that at least the secondary females of polygamous males raise fewer young than monogamously mated females (*e.g.*, CURIO, 1959; VON HAARTMAN, 1969; WITTENBERGER, 1978; ALATALO *et al.*, 1981). We obtained the same result in marsh harriers. The numbers fledged were not significantly different where females engaged in polygamous and those in monogamous relationship were compared. However, secondary females raised signifi-

cantly fewer young than monogamous females (ratio $x_1 = \frac{2.3}{3.0} = 0.77$), and also less than monogamy-females starting clutches at the same time of year (ratio $x_2 = \frac{2.3}{2.7} = 0.87$). If breeding success was a good measure of relative fitness, any genetic determinant of the tendency to mate with males already mated should vanish in the population according to the polygyny-threshold model. The benefits compensating such females for a supposedly reduced fitness have been the subject of considerable recent debate and speculation (WEATHERHEAD & ROBERTSON, 1979, 1981; WITTENBERGER, 1979, 1981; HEISLER, 1981; SEARCY & YASUKAWA, 1981).

In this section, we discuss some points relevant to this debate in the light of the marsh harrier results. We further challenge two basic premises of the polygyny-threshold approach, (a) that annual breeding success reliably estimates lifetime reproductive output, and (b) that only female decision is involved in differences in mating status.

6.1. Offspring survival.

The benefits compensating some females for a reduced breeding success might in the first place be sought in differential survival of the young until they enter the breeding population. Fledglings of secondary females might in principle have better chances of survival than those of monogamous pairs. We have not been able to collect this information in marsh harriers, nor has it been considered in any of the other field studies on avian polygyny. Yet it is known that considerable variation in post-fledging survival occurs. Some of this variation may be predicted by fledgling condition (*e.g.* DRENT & DAAN, 1980). If in marsh harriers survival till reproductive age would be contingent on the condition at fledging, it is likely that at least the sons of secondary females would face even lower survival rates after fledging than the sons of monogamous parents (Fig. 16). The ratio between offspring productions of secondary and monogamous females may thus even be overestimated by basing it on the number of young fledged rather than young contributed to the next breeding generation. On the other hand, the reduction of breeding success of secondary females was mainly due to malnutrition leading to increased male nestling mortality and a preponderance of daughters fledged. These may have had higher average survival rates than monogamous offspring with their more equal sex ratio (Table 9). A further complication is the dependence of post-fledging survival on fledging date known in several other bird species including raptors (PERRINS, 1970; CAVÉ, 1968; DAAN *et al.*, in prep.).

We have no basis to assume that the higher nestling mortality and smaller numbers of young fledged by secondary females are compensated by higher postfledging survival till reproductive age. Yet it is crucial to measure this survival if a full evaluation of the polygyny-threshold model and the 'sexy son hypothesis' (see 6.2.) is to be obtained.

6.2. Offspring quality.

If secondary females indeed produce fewer surviving offspring than females of monogamous males, they may be compensated in the second generation by better chances of reproduction due to a superior genetic make-up of their progeny, as proposed by WEATHERHEAD & ROBERTSON (1979). These authors specified the presumed superiority as being due to the sons, who might inherit attractiveness character from their fathers (the 'sexy son hypothesis'). This specific model was extended by HEISLER (1981) to cover benefits potentially obtained in subsequent generations. Others have presented arguments that the specific advantage of such offspring may not be in sexual attractiveness but in the capacity to obtain better territories (WITTENBERGER, 1981), or to care better for their young (SEARCY & YASUKAWA, 1981). WITTENBERGER (1981) extensively reviewed the available field data on the subject, nearly exclusively dealing with territorial songbirds. He found no compelling evidence that there are variations in male quality involved independent of the territories they hold.

Among marsh harriers, we found evidence of different rates of prey return to the nests. Bigamous males in all phases of the breeding season brought more prey than monogamous males (Fig. 12). In the three individuals observed on their hunting trips, this difference was found to be due to variations in the net hunting yield (prey returned/hour of hunting) (Fig. 13) rather than in the time spent hunting, which reached the same plateau value of 7-8 hours per day in all birds during the nestling phase (Fig. 10). This definition of hunting yield even underestimates differences in prey biomass delivered, since polygamous males tended to bring larger prey than monogamous males (Table 4). There was thus considerable variation in male hunting performance and parental care, associated with their mating status. This variation was independent of territory quality, since the males hunted outside the breeding territories (Fig. 7) and defended no hunting territories. In fact their hunting ranges showed a great measure of overlap (Fig. 9). We can not be sure that hunting yield is unaffected by nestling demands, such that polygamous males with many nestlings would raise their hunting yield at the expense

of other factors affecting their fitness. Field experimentation would be required to solve this issue.

We remain further uninformed about the genetic basis of such variation in male performance. Such evidence is obviously needed for a proper evaluation of the proposition that secondary females compensate for fewer offspring by better genetic quality of the offspring. In none of the polygyny studies so far is any independent information of heritability of quality aspects available. Genetic improvement by polygynous mating can not be demonstrated on the basis of breeding success rates (WEATHERHEAD & ROBERTSON 1979). The theory can only be tested with independent genetic evidence. Of its three alternative specifications (improvement by male attractiveness, territorial quality or parental care), the latter is a likely candidate for the benefits accruing to the offspring of polygamous marsh harrier.

6.3. Parent future reproduction.

Not the annual breeding output but the lifetime reproductive output determines the relative fitness of breeding strategies. The reduction in expectation of future offspring due to the efforts in any attempt at reproduction has been termed 'parental investment' (TRIVERS, 1972; MAYNARD SMITH, 1977). Such reduction may be due to increased chances of mortality when a great deal of effort is devoted to producing eggs or raising the young. TRIVERS' theory predicted that the sex with small parental investment may engage in polygamous relationships with several partners. A test of this theory would require the empirical establishment of probabilities of parental survival as contingent on mating status. Such information is so far unavailable for studies of avian polygyny, including the marsh harrier.

We have, however, a strong suspicion that the opposite of TRIVERS' prediction is true in raptorial polygyny. It is usually the male who provides both the female and the nestlings with food during the breeding season, and in terms of energy spent on the young, certainly puts in much more effort than the female. Yet it is also generally the male who mates with two or more partners simultaneously. The fact that both polyandry and polygyny occur in raptors where male parents feed the young (NEWTON, 1979) suggests that differential investment by the sexes is not predictive for either strategy.

In this context we wish, however, to raise the possibility that secondary females are compensated for their reduced breeding success by increased chances for future reproduction. Secondary females are generally

younger than primary or monogamy-females in most avian polygynous systems (WITTENBERGER, 1979). While this may be a consequence of increased mortality resulting from greater parental care (Fig. 15), it is at least as likely that the secondary status is only temporary. Many raptor species have pairbonds persisting from year to year and at least in favourable habitats there is a consistent tendency to return annually to the same breeding place (NEWTON, 1979). It is quite possible that secondary females have a good chance of becoming the primary female of their mate next year and from then onwards receive the full fitness benefits from being the primary female of a high quality male. It was shown in marsh harriers that such primary females have to spend relatively little effort obtaining food for their young (Fig. 15) and yet raised more nestlings than monogamy-females (Table 7), due to male preference for its primary nest and thereby reduced nestling mortality.

The marsh harrier is not an easy species to study survival rates and lifetime reproductive output. For a true understanding of avian polygyny, we feel, however, that we should heed the warning implicit in TRIVERS' (1972) argument, that effects of breeding strategies on these demographic features should be analysed. Only when it can be demonstrated that lifetime reproductive output is reduced in females sharing males already mated, a recourse to theories of genetic improvement of the offspring is called for.

6.4. Sex ratio and parent decisions.

The options open to individual birds taking their mating decisions remain virtually unknown in most field studies. The polygyny-threshold model (VERNER & WILSON, 1966; ORIAN, 1966; WITTENBERGER, 1979) assumes that any female has at least the option of choosing between secondary status with a polygamous male and mating monogamously. In systems where the sex ratio in the population is close to unity this may be true, but we have no basis for assuming that the average monogamous pair represents the real alternative a secondary female might have chosen. Had she opted for monogamy, she would have mated with a male which in reality remained unmated, on a territory which in reality remained unproductive. Such males would represent submarginal breeding situations and breeding success would on average have been less than in monogamous pairs. WITTENBERGER (1981) realized that secondary females should be compared with monogamy ♀♀ in the same habitat, of the same age, starting at the same time of year. Using such marginal pairs for comparison is better than using the average monogamous pair,

but even this may overestimate the relative fitness associated with the alternative option for secondary ♀♀.

In breeding populations where the sex ratio is skewed towards the females the polygyny-threshold model would not apply since the alternative for secondary females would be non-breeding (EMLEN & ORING, 1977). In marsh harriers there was a slight but significant preponderance of male fledglings (Table 9), although in 44 completely fledged broods the primary sex ratio was virtually unity (96♂♂, 93♀♀). However, females mature more rapidly than males, and unless females suffer greater mortality than males, this would lead to a preponderance of females in the breeding population. A preliminary calculation, assuming that the sexes breed for the first time when reaching adult plumage (♀ in 2nd, ♂♂ in 3rd year; NEWTON, 1979), and that both sexes suffer annual mortality rates of 54% in 1st, 53% in 2nd, 42% in 3rd year and 40% thereafter (calculated from ring recoveries from Finland, Holland and Germany (GLUTZ VON BLOTZHEIM, 1971) gives a sex ratio of breeding females per male of 1.87. An overproduction of male fledglings (55% ♂♂), as we found, would slightly compensate for this bias, but still yield a breeding sex ratio of 1.53 ♀♀ per ♂. A similar situation was found in the Hen harrier in Orkney, where females were far in excess of males in the breeding population, the sex ratio (1.81 ♀♀ per ♂) being greater than the ratio (1.16 ♀♀ per ♂) at fledging (BALFOUR & CADBURY, 1979).

Given such imbalance in the sex ratio, polygyny could be considered a byproduct of different rates of maturation of the sexes. The female's options are constrained by unavailability of free males. This transfers the question to the stability of different life-history strategies of the sexes. The females probably put in a more constant annual effort in reproduction, the males may often refrain from early breeding (although immature male Hen harriers are certainly able to breed; BALFOUR & CADBURY, 1979) and be compensated by polygynous matings later in life. We shall come back to this in section 6.5., but we first need to digress on the male's role in the decision process.

Polygyny theory, rooted in the theory of sexual selection (DARWIN, 1871; CAMPBELL, 1972), has axiomatically assumed that it is only the female who selects her mate, and that it is selection of males with the disadvantageous property of being mated already that has to be accounted for. However, it is likely that part of the decision process is the male's. Male marsh harriers which mated with two or more females had higher hunting yields (Fig. 13) and brought more (Fig. 12) and larger (Table 4) prey to their nests than monogamous males and yet suffered

higher mortality in their secondary broods. In monogamous males, had they opted for polygamous status, nestling mortality would probably have been even larger. The time and effort they would have spent on feeding a secondary female throughout incubation and her nestlings till death of starvation would have been wasted. Although polygamous males obtained twice the annual breeding success of monogamous males (Table 7), it is likely on functional grounds that other males may have actively refrained from taking on the burden of a second female. Incidental observations of aggressive encounters between male and female marsh harriers during the courtship phase support this possibility.

Female parental quality may affect which females become engaged in polygamous relationships. We observed no differences in hatching success of the eggs (Table 7), and female incubation performance may not be a main variable. However, there were differences in the size of prey females brought to the nestlings (Table 6), suggesting that primary females may be more successful hunters than others. It is likely that males opting for polygamy had reason for selecting their mates, even without recourse to a nearly untestable genetic theory.

Further decisions by the male once polygynously mated involve the distribution of prey over its females and nests. During the nestling phase there was a clear preference for the primary nestlings (Fig. 14). Of course one may again propose that primary fledglings would benefit their father by better genetic quality than secondary fledglings (a sort of 'sexy daughter hypothesis'). A simpler and more readily testable hypothesis is, however, that early fledglings have better post-fledgling survival chances than late ones, as in many other birds species (*e.g.*, PERRINS, 1970; CAVÉ, 1968). By fledging date alone they may represent more fitness value to the polygynous male than his secondary offspring.

Male decisions in the distribution of prey over his females may further be involved in the sizes of clutches laid. From another raptor, the European kestrel (*Falco tinnunculus*) we know that prey deliveries are more frequent during courtship and laying than during incubation and that the delivery frequency during laying is a major factor determining clutch size (MASMAN *et al.*, in prep.). Secondary clutches are started on average 13 days after initiation of primary clutches (Table 1), or only ca 5 days after primary clutch completion. It is possible that female competition for prey deliveries around this time (see NEWTON, 1979, p. 33) leads to a slight reduction of mean primary clutch sizes observed (Fig. 4). The slight increase in secondary clutch sizes as compared with those of monogamous pairs laying at the same date may reflect the better hunting performance

of the polygamous males. Unfortunately we have no data on hunting yield and prey deliveries in the laying phase to test this hypothesis.

6.5 Stability of polygamy in raptors.

Hence, there are various ways in which males may participate in decision processes concerning both their mating status and the differential care for their mates and offspring. We expect then, that polygyny is a consequence of general life history strategies which obey separate optimization criteria for males and females. That these criteria are different is almost certainly related to task differentiation between the sexes. Female performance in production of eggs and in incubation is presumably subject to little interindividual variation. Males on the other hand differed considerably in their performance in bringing food to the nest, although their effort in terms of daily hunting time was approximately the same (Fig. 10). We suggest that the difference is due to large phenotypic variation (*e.g.*, by learning) in hunting performance, and small variation in the physiological constraints on egg production and incubation.

If both sexes work equally at optimal capacity (ROYAMA, 1966; DRENT & DAAN, 1980) we expect that the optimal number of offspring to invest this effort in would be rather invariable for females (close to 5 in the case of the marsh harrier) but highly variable (*e.g.*, between 1 and 10) for males. Some variance may be added to individual female optima by their ability to feed older nestlings, but this is small relative to the variance in the males' contributions. If variation in hunting performance is indeed largely due to learning, it may be understood why young males tend to refrain from polygamous mating (as in hen harriers; BALFOUR & CADBURY, 1979) or from breeding at all (deferred maturity as in marsh harriers), while older adults aim at simultaneous matings with two or more females.

Assuming a relatively invariant optimal working capacity we can try to analyse qualitatively how male variance in hunting performance should affect his mating decisions (cf. Fig. 17). The annual foraging return of a male is partly needed to cover the metabolic needs of his female to produce and incubate the eggs. The prey he is able to catch in addition during the season contribute to the chances of offspring surviving till fledging. We assume the function is S-shaped (Fig. 17A), with less steep slopes near the minimum and maximum offspring production: near the lower limit, extra prey will go to nestlings dying later and thus be wasted; near the upper limit slight variations in prey return will be compensated by

hunting efforts of the females. The conclusions are, however, independent of the precise shape as long as the curve is monotonic. In Fig. 17B, C, we have plotted the number of broods raised per female and per male as a function of σ foraging return for three hypothetical situations: Biandry ($2\sigma\sigma$, 1♀), Monogamy (1σ , 1♀) and bigyny (1σ , $2\text{♀}\text{♀}$). The curve for females in bigyny is obtained by doubling for each Y-value the corresponding X-value. The curve for females in biandry is obtained by

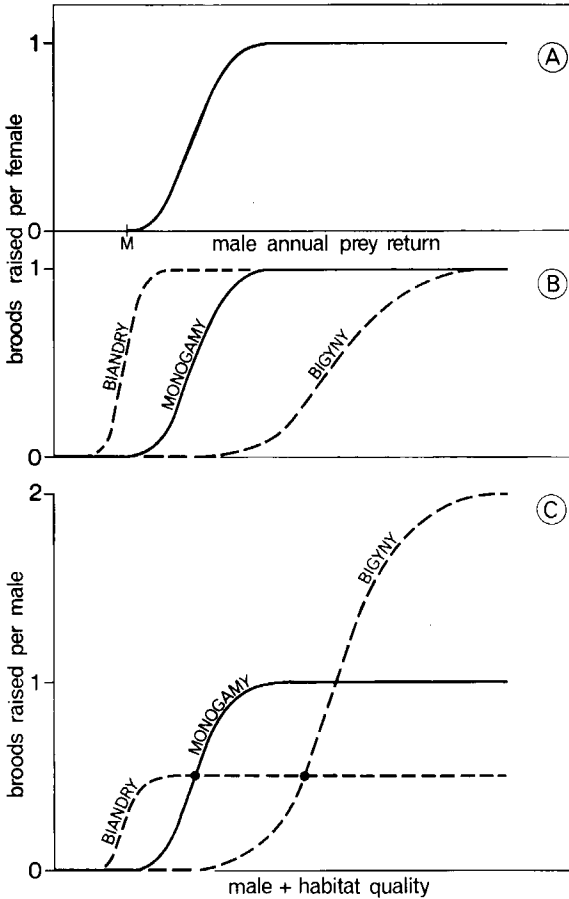


Fig. 17. A model depicting breeding success as a function of male hunting performance for various mating decisions. A Relative brood size raised per pair as a function of total annual prey return of a male working at optimal capacity. Production is zero up to a minimum prey return M needed to sustain the female, and has an s-shape towards maximum brood size raised (see text). B. Breeding success per female for monogamy, biandry (2 males) and bigyny ($1/2$ male). C. Breeding success for males obtained from B by halving (biandry) or doubling the Y-values.

multiplying each X-value with $1/2$ (Fig. 17B). Male offspring production (Fig. 17C) is then derived from these curves by doubling the Y-values of the female bigyny curve, and by halving those of the female biandry curve. From Fig. 17C it can now easily be seen that with decreasing quality there is a sequence of male strategies, from bigyny, via monogamy to biandry representing the optimal decisions. For very low quality males non-breeding may be the optimal strategy in a particular year. For the females, the same mating patterns become acceptable in sequence with increasing male quality: non-breeding, biandry, monogamy, bigamy. Of course the model can be extended to polyandry and polygyny involving more than 2 partners of the same sex.

If the sex ratio in a population is close to unity, we can see that large variation in male quality would lead some males to opt for bigynous, others for monogamous relationships and some, presumably inexperienced males for non-breeding. Since male foraging return is partly a function of environmental quality, large variation in the latter may thus be inductive for polygyny, as postulated by EMLEN & ORING (1977). If all males are equally poor, biandry should be the stable solution, preferred by both males and females. However, their annual production would be small, since at least half of the females would not participate in reproduction. If all males are equally good, they all would opt for bigyny and there would not be enough females around to attract. In such situations we may expect the females' preference to select for monogamy as the general pattern.

It has been pointed out (NEWTON, 1979) that polyandry requires inter-male tolerance, while polygyny may be favoured by inter-male aggression. Raptor species with wide distributions including rich habitats will thus be dominated by polygynous traits disabling them to successfully exploit poorer habitats. Only species living isolated in poorer environments such as the Galapagos hawk (FAABORG *et al.*, 1980) and Harris' hawk in Arizona (MADER, 1975) may have developed the behavioural prerequisites for polyandry as a mating system. In other species, where only the options of polygyny, monogamy and non-breeding are open, we expect that rapid maturation as in the smallest raptors would act against variation in male hunting performance and thus against polygyny. Likewise, slow maturation as occurs in the largest may not lead to skewed breeding sex ratio's and polygyny. Intermediate size and speed of development, together with a specialization in relatively rich, early succession stages (ORIAN, 1969) may have made the harriers among raptors (NEWTON, 1979) especially prone to develop polygynous tendencies.

SUMMARY

1. Theories postulating that sexual task differentiation may lead to polygamy such that the sex investing the least effort in raising the offspring, engages in simultaneous matings, contrast with polygyny in raptors where the male provides most of the food for its females and nestlings. A field study was undertaken to describe parental effort and success in marsh harriers of different mating status to elucidate this controversy.

2. Data on clutch size and laying date were collected on 421 nests in two Dutch land reclamations, Flevoland and Lauwersmeer. 156 nests were known to have monogamous parents, 30 males had two females and nests. Bigamous males raised on average twice as many fledglings (5.7) than monogamous males (3.0). However, their primary females had more success (3.5) than secondary females (2.3), related to increased nestling mortality in secondary nests (Table 7). Male fledglings were significantly heavier in primary than in secondary nests (Fig. 16).

3. Nest observations made on 22 nests (5 of monogamous, 17 of polygamous males) revealed that daily prey deliveries by males were fewer in mono- than in bigamous males (Fig. 12). The latter delivered prey by preference to their primary nests (Fig. 14). The prey delivered by a trigamous male were consistently larger than those of a bigamous and monogamous male in the same area (Table 4).

4. Time budget observations revealed that hunting effort was maximal in the nestling phase (ca 8 hrs foraging per day for all three males observed (Fig. 10); at other times of year foraging was reduced in early morning and late afternoon (Fig. 11). Net hunting yield (prey brought to nests per hour of hunting) increased in three males with their number (1, 2, or 3) of mates (Fig. 13). With progress of the breeding season, male hunting ranges extended further outside the breeding territories (Figs. 7, 8, 9) and had a great measure of overlap, suggesting that territory quality was not a major factor in male hunting yield.

5. Secondary females participated in provisioning for the nestlings more than primary or monogamy-females (Fig. 15), thus compensating for reduced male prey deliveries.

6. Classical polygyny theory addresses the question of female choice: which benefits compensate a secondary female for reduced breeding success by mating with an already paired male? Several hypotheses (enhanced offspring survival, offspring genetic quality, parent chances of future reproduction) are discussed, but evidence is nearly completely lacking (ch. 6.1-3).

7. An alternative approach stresses the male's role in the decision process. Males may have more interindividual variation in their capacity to bring food than females in their capacity to lay and incubate eggs. Optimal strategies for males would then range with increasing quality from non-breeding via polyandry and monogamy to polygyny (Fig. 17). In species like harriers, non-breeding may be optimal for yearling males with submaximal hunting skills, thus creating a skewed sex ratio forcing some females to accept secondary status as mate of older, high quality males. Polygyny is then associated with slower male than female maturation. The evolution of polyandrous traits in species living isolated in poor environments is likewise explained by this model.

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ZUSAMMENFASSUNG

1. Polygynie bei Greifvögel, wo das ♂ das Hauptanteil in der Nahrungsversorgung von ♀ und Junge hat ist in Widerspruch mit der bisherigen theoretischen Auffassung dass die Arbeitsteilung zwischen den Geschlechtern in solcher Weise zu Polygamie führt dass das Geschlecht das am wenigsten in die Nachkommenschaft investiert, sich mehrere Partner leisten kann. Eine Freilanduntersuchung wurde gemacht um Arbeitsteilung und Bruterfolg by mono- und polygyne Rohrweihen zu beschreiben als Grundlage für ein besseres Verständnis von Paarungssysteme bei Greifvögeln.