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THE UNIVERSITY OF ALBERTA

THE INFLUENCE OF DOMINANCE STATUS ON MATE CHOICE IN BLACK-BILLED MAGPIES (*Pica pica*)

by

PETR ERNST KOMERS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE INFLUENCE OF DOMINANCE STATUS ON MATE CHOICE IN BLACK-BILLED MAGPIES (*Pica pica*) submitted by PETR ERNST KOMERS in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

Supervisor

W. Bruce McGillivray

John R Spence

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Date Nov. 2, 1987

Abstract

The main goal of this study was to investigate the influence of both dominance status and age on mate choice and pairing success. Dominance hierarchies were recorded in unisexual groups of ten black-billed magpies (*Pica pica*). The hierarchies were significantly linear among males but not among females. In groups of five of mixed sex, females often changed rank with each other, whereas males never changed rank with another male. I suggest that this difference in dominance relationships between males and females may explain the different pairing patterns found in the two sexes: males in the alpha dominance category paired more often than subordinate males, whereas dominance status did not influence pairing success of females. In choice experiments females chose adult more often than juvenile males, and dominant more often than subordinate males. Males did not discriminate between the two female age groups. I propose that such differences in the manifestation of choice between males and females may be due to different degrees of variation in male and female reproductive variables: adult and juvenile males differed in most of the recorded variables of the reproductive cycle, whereas females did not differ between the two age groups. I also suggest that females preferred adult over juvenile males because adult males invested more in parental care than juvenile males in this study. Since dominant and subordinate males did not differ in any of the variables of reproductive performance, the preference of females for dominant males could not be explained by this study.

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I. INTRODUCTION

The role of mate choice in sexual selection was discussed as an aspect of natural selection by Darwin (1871) and later expanded upon by Fisher (1930), and many workers in the more recent literature. Recent discussions address a variety of problems about mate choice including the sex of the chooser and the relative frequency of matings obtained by members of a given sex, age or dominance category (for a review see: Dewsbury 1982; Halliday 1983). In order to demonstrate the distribution of matings in different sex, age and dominance categories it is essential to be able to distinguish such groups morphologically and/or behaviourally. In the wild, different age and dominance categories may be confounded with some of their correlates such as territory size or territory quality. Only in captivity is it possible to separate such confounding factors from the social status of the individual in question. Moreover, once mating preferences have been demonstrated, one is left with the question of the actual reason for the preference. Is preference based on morphology (e.g. are "preferred" individuals more easily located (Ryan *et al.* 1981) or does preference have a functional significance (e.g. do "preferred" individuals provide better parental care (Trivers 1972; Yasukawa 1981)?

The nature of mate choice in black-billed magpies, *Pica pica* was a central question in this study. Magpies pair monogamously and both parents care for the young (Baeyens 1981; Reese 1982). Trivers (1972) suggested that in those species with equal parental investment both sexes should be choosy. Thus, the degree to which each sex exhibits selectivity becomes an important question to address. Superimposed on this problem is the influence of both age and dominance status on the choices made. Two age classes (adults: >1 yr old, juvenile: <1 yr old) can be distinguished readily in magpies (Erpino 1968; Reese & Kadlec 1982) and dominance status, reported to be an important factor in the social structure (Baeyens 1981; Reese 1982; Scharf 1985; Eden 1987) and reproductive success of magpies (Baeyens 1981; Reese 1982), can be determined by observing the outcome of interactions, making this species an appropriate subject to study the influence of dominance status and age on mate choice.

Before the impact of dominance status on mate choice can be addressed, dominance relationships within and between age and sex groups have to be determined. Although many studies have reported dominance hierarchies and speculated on their function in magpies (Baeyens 1981; Reese 1982; Scharf 1985; Eden 1987), none has demonstrated the linearity of such hierarchies; linearity was always assumed. In the second chapter of this study I test for the linearity of the dominance relationships recorded in groups of magpies.

Once dominance relationships and their influence on mate choice were known the function of mate choice was investigated. I predicted that if one or both sexes exert choice, the preference would be for those individuals that promise the greater parental contribution (Trivers 1972). Theoretically, such differences in potential parental quality could be found either between dominance classes or between age groups. The problem of parental quality is addressed in the fourth chapter.

The study animal

Black-billed magpies are a species amenable to study in captivity (Scharf 1985; Reese 1985). They adapt quickly to captive conditions, readily accept food, tolerate conspecifics in the same pen, and usually form pairs and engage in breeding activities if provided with the necessary material (nest support, nesting material). Furthermore, magpies are abundant in Edmonton, viewed as a nuisance species by most of the human population, and are relatively easy to catch in large numbers. All these factors made it feasible to conduct this study of the causes and consequences of mate choice in black-billed magpies in captivity.

It is difficult (but not impossible) to establish the nature of dominance relationships among all members of flocks of wild living magpies. Hierarchies are easier to document among birds in captivity, since all the birds are present at all times and interactions can be evoked among all individuals. This was a major reason for using captive birds. Furthermore, variables such as food availability, composition of flocks with respect to age and sex ratios, and "territory" quality could all be controlled under the captive situation - a necessity for answering the questions posed. Thus pair-formation could be investigated in a situation where each individual had the same opportunity to exert a choice, and not be biased by the presence or absence of members of a certain age and sex group. Also, because "territory" quality was held constant its influence on mate choice or parental investment was excluded.

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II. DOMINANCE HIERARCHIES

DOMINANCE RELATIONSHIPS AMONG BLACK-BILLED MAGPIES: DO ADULTS DOMINATE ?

ABSTRACT

The impact of sex and age on the nature of dominance hierarchies in black-billed magpies, *Pica pica*, was investigated. Dominance hierarchies were looked for in 11 unisexual groups of 10 captive magpies, and 32 mixed-sex groups of five captive magpies. In all nine unisexual groups of 10 males observed, strongly linear hierarchies were found. Of the two groups of 10 females observed, one was not linear and the other only marginally so. The occurence of circular dominance relationships (reversals) was 50 times greater in female than in male groups. The implication of the difference in dominance relationships between the sexes on the breeding biology of magpies and its generality for other corvids are discussed. In all 32 groups of five magpies of mixed sex and age the most dominant bird was a male (juvenile in 23 cases and adult in nine). Based on these observations the asymmetry hypothesis, to explain the dominance of adults by juveniles, was rejected. The hypothesis that such an anomaly in dominance relationships is an artifact of the captive situation was also rejected. The reasons for the apparent contradiction between the higher dominance status of juvenile males in the wild and their lower reproductive success are discussed.

INTRODUCTION

Social dominance influences a number of variables affecting the population biology of birds, including survival in time of food shortage, characteristics of dispersal, use of habitat, and reproductive success (for a review see: Dewsbury 1982; Kaufmann 1983). For most species of passerine birds in which social dominance has been investigated, adults of a given sex dominate juveniles (e.g. Pinowsky 1965; Ficken & Ficken 1967; Rohwer et al. 1981; Ficken et al. 1981). Exceptions, however, have been reported: at food sources, juvenile male house sparrows, *Passer domesticus*, won encounters with adults of the same sex (Simmons 1954, Watson 1970), and juvenile male black-billed magpies, *Pica pica*, dominated adults at feeding stations during their first winter (Reese 1982).

Size has been correlated with dominance status in magpies, larger individuals dominating smaller ones (Scharf 1985a). Yet size dimorphism between adult and juvenile male magpies is an unlikely explanation for Reese's (1982) observations, because the size distributions of adults and juveniles of this species are similar (Scharf 1985a). Parker (1974) suggested that the dominance status achieved by birds of different ages is related to the different benefits each gains from an agonistic encounter. Adult male magpies being more experienced are consequently more efficient foragers (Reese 1982). Thus, they would have relatively less to gain over a fight for food than would juvenile males. If the outcome of an agonistic interaction were the reflection of such an asymmetry in the relative benefits to the two contestants, then body size would not necessarily predict wins and losses, and consequently dominance status at a food source (Maynard Smith & Parker 1976). Reese (1982) suggested that the asymmetry hypothesis may explain this anomalous dominance relationship between adult and juvenile male magpies. Assuming that the asymmetry hypothesis holds, then birds held under the same environmental conditions and with access to the same food source, should win interactions according to their fighting ability alone, because the importance of differences in relative foraging success would be cancelled by the presence of food ad libidum. Under these conditions one would expect adult male magpies to win such encounters, if not as a result of differences in body size then because of their greater experience in fighting. Reese (1982) predicted that adult males should dominate juveniles in captivity because the asymmetry in foraging benefits would be eliminated.

Differences in dominance status have been found not only between age classes but also between sex classes, male magpies usually being dominant to females (Baeyens 1981b; Reese 1982; Scharf 1985a). This may be due either to the larger body size of males (Reese & Kadlec 1982; Scharf 1985a) or their greater aggressivity (Scharf 1985a). Baeyens (1981a,b) suggested that as males are the more active sex in territory establishment and defence they must also be the more dominant sex. The role of dominance status in reproduction has been addressed in magpies (Baeyens 1981b; Reese 1982); dominant individuals are reported to be more successful than subordinates, because they gain territories of better quality (lower level of predation) and produce more young which fledge earlier and have a higher survival rate. These studies, however, did not consider dominance status of males and females separately but used groups of mixed sex to determine the relationship between dominance rank in the group and subsequent reproductive success. Although the roles (e.g. incubation and territory defense) of the two sexes differ in many ways during the reproductive cycle (Labitte 1953; Bährmann 1963; Erpino 1968; Baeyens 1981a,b; Mugaas & King 1981), the impact of dominance rank on these roles has not been investigated in either sex separately. Reese & Kadlec (1985) found that there was greater variance in reproductive success among males than among females, age of males influencing reproductive success more than age of females. Since the two sexes have different roles in reproduction, and exhibit different variances in reproductive output, it is essential to understand the nature of dominance relationships and how they are established in the two sexes separately before investigating the influence of dominance status on reproduction in general.

In this study the influence of sex and age of dominance relationships within groups of black-billed magpies was investigated and the relevance of the asymmetry hypothesis to these relationships examined.

METHODS

This study was conducted over two seasons (1985/86 and 1986/87) in a large outdoor aviary at the University of Alberta's Bioscience Animal Centre, 15km south of Edmonton, Alberta. Between April and September 1985, 80 magpies were captured using either circular funnel traps (Alsager et al. 1972) or nooses arranged around a decoy (Scharf 1985b). All birds were measured, weighed, and individually marked with unique combinations of coloured bands. Their sex and age were determined according to Scharf (1987). The 40 males were separated into four groups of 10 birds each, two of which were adults and two were juveniles. The 40 females were also kept in groups of ten, one of which contained the only five adults available. The birds were accommodated in an aviary which consisted of 16 pens arranged into two rows facing out from a central building. Eight pens in one row faced north, the others south (Fig.II-1). Each pen measured 5.8 X 2.4 X 2.1m and was connected to the sheltered portion by a door measuring 0.8 X 0.5m. The inside portion measured 2.1 X 2.4 X 2.1m. Solid partitions separated the pens, visually isolating birds in one pen from those in adjacent pens.

Dominance Hierarchies in Unisexual Groups of 10 Magpies

At first, each group of 10 birds was housed in two adjacent, interconnected pens, one pen being too small for 10 birds. Hierarchies were allowed to develop in each of the four groups of males for a period of 2 weeks. Ranking of the birds in each hierarchy was subsequently undertaken by first depriving the birds of food overnight and then recording wins and losses over a small food source. The groups were observed from a movable blind placed adjacent to the outside portion of the pens. After 8 to 10 hours of observation most of the 45 possible dyads showed at least one overtly agonistic interaction. Birds with missing interactions were ranked so that the number of possible reversals was minimized (Appleby 1983). The hierarchies so recorded were tested for linearity according to Appleby (1983). To verify the stability of the hierarchies, each of the four groups was observed for 1 to 2 hours 14 days after initially recording the hierarchy. The same procedure was followed for ranking

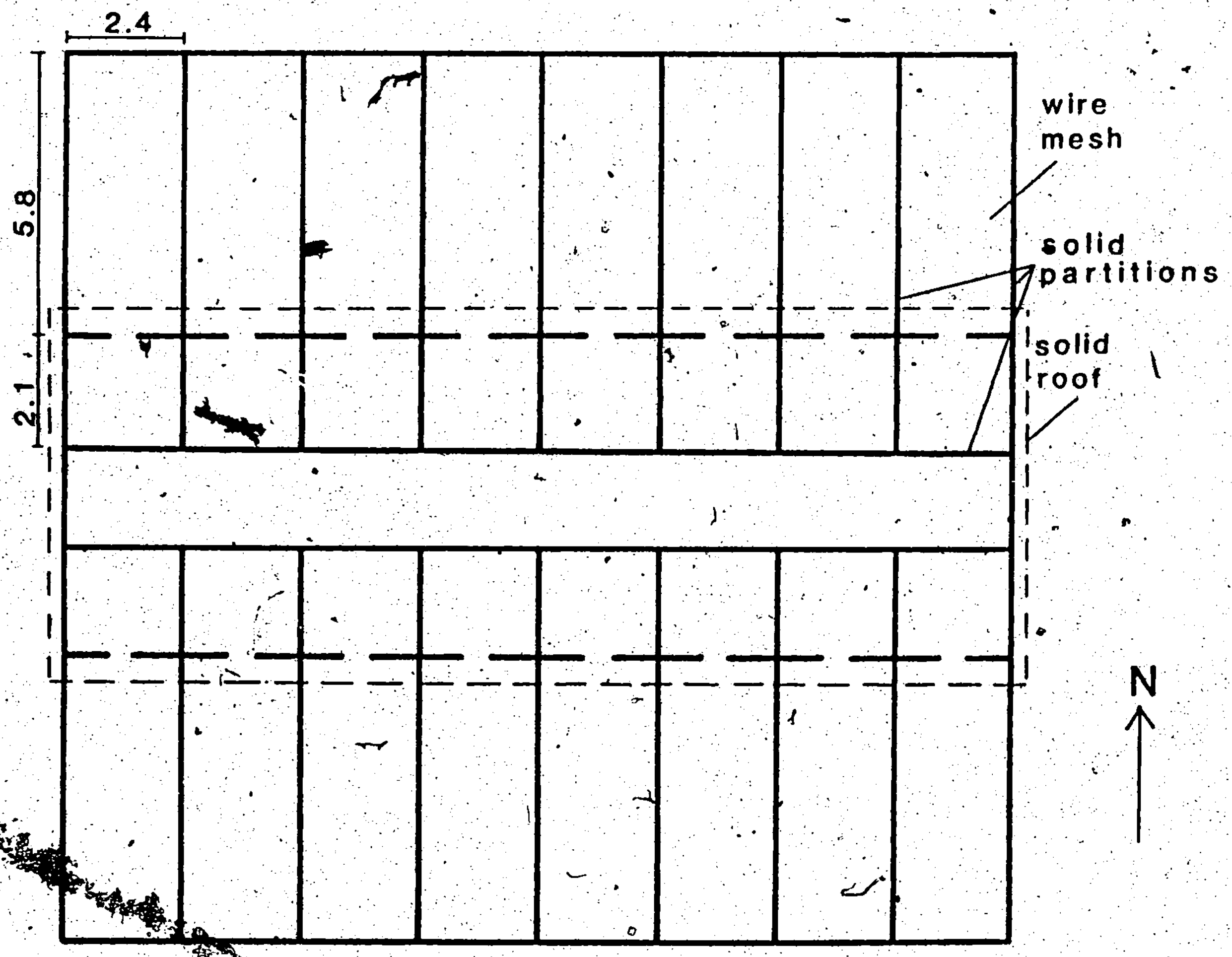

Figure II-1. Aviary used for housing groups and pairs of magpies. Measurements in meters.

birds in two groups of females. Females in the other two groups were not ranked.

Dominance Hierarchies in Groups of Five Magpies of Mixed Sex

At the end of January 1986 the birds from the groups of 10 were distributed in the 16 pens so that each pen housed five birds. The distribution was as follows: of the juvenile males, one group (eight of ten) was distributed in the south row of pens, and the other along the north row. They were distributed according to the dominance status of the individuals within each group, highest ranked in the westernmost pen to lowest ranked in the easternmost pen. The two extra birds were of intermediate ranks (four to seven), one being placed in each of the two most western pens containing the juvenile males ranked one and two. Adult males were divided up similarly but distributed inversely (highest to lowest ranked birds from east to west). The two remaining adult males of intermediate ranks were added to the most dominant adult males at the east end (Fig.II-2). Females were distributed randomly, except to avoid placing them with males caught at the same trapping site at the same time.

The groups of five were given 2 weeks to establish hierarchies and then the birds were ranked in each of the 16 groups as described above for the groups of ten. Each flock was observed until each bird was involved in at least two agonistic interactions with each of the other members of its group. If, after 3 hours, a specific bird could not be assigned a rank, that bird was exposed individually, in the outside portion of its home pen, to each of the others in the group and outcomes of the interactions recorded.

The Second Season

In the second season, another 30 males and 30 females were captured and measured as described above. Ten adult males and 10 adult females, that had successfully paired in the previous season were also used. Note that six of the 10 adult males were juveniles of the previous year and the remaining four were captured as adults. Hierarchies established in the three groups of 10 males caught in 1986 as well as among the 10 males from 1985 were documented in the same manner as described above for 1985. In addition, to check for a

1985

north

rank								
1	J1	J2	J3	J4	J5	A3	A2	A1
2	J6		A7	A6	A5	J7	J8	A4
3	A10						A8	J10
4		A9						
5								

south

rank								
1	J1	J2	J3	J4	J5	J7	J8	A1
2	J6		A7	A6	A5	A3	A2	
3	A10							
4		J9						J10
5		A9					A8	

1986

north

rank								
1	J1	J2	A9	J4	A4	J7	A8	A1
2	J5		J3	A6	J6	A3	J8	A5
3	A10	A7					(A7)	
4		J9						J10
5								

south

rank								
1	J5	J2	J3	J4	J7	J8	J9	A1
2		J6	A7	A5		A3	A2	J10
3		A8			A4		(A10)	A6
4	J?							
5	A10							

Figure II-2. Age of male magpies in the dominance hierarchies (n=32) recorded at the end of the season for groups of five birds of mixed sex. The distribution of the groups is shown in relation to the aviary (cf. Fig. 1). A = adult male, J = juvenile male, blank box = female, superscript indicates rank in groups of 10, ? = male with unknown ranking introduced after the death of the first male (J1). Individuals in parenthesis show original position and rank before moving (see text.). The missing male in each series of pens in each year died during the season (1985 south: A4; 1986 north: A6; south: A7). One juvenile "male" (1985 north: J9) was infact a female.

possible captivity effect, five adult males caught in 1985 and five adult males caught in 1986 were joined in one group of ten, after their rank in the initial group of ten adult males was known. Subsequently, a hierarchy was recorded. No attempt was made to rank females in any of the four groups. Thus, over the 2 years of the study, hierarchies were established in nine groups of males and two groups of females. To avoid interactions between males and females that were familiar with one another, the adult females from 1985 were distributed among the eight groups of five in the south row, and the adult males from 1985 among the eight groups in the north row. This distribution was arranged as described for 1985 but undertaken earlier (at the beginning of November 1986) and the hierarchies established in each of the 16 pens were recorded 1-week later.

RESULTS

Dominance Hierarchies in Unisexual Groups of 10 Magpies

During this study, the dominance relationships among magpies in 11 unisexual groups consisting of 10 birds each were recorded (see Appendix 1). The linearity (Appleby 1983) of the dominance hierarchies established in all nine groups of males was significant (K values: mean 0.814, range 0.53-0.93; $P<0.05$). Only in one group (Appendix 1, Table VI-8) was a single male able to dominate two males ranked higher than it in the hierarchy (hereinafter called "reversals" <u>sensu</u> Appleby 1983). Despite more hours of observations of females (12 hrs per group vs 10 hrs for males), linearity of the dominance hierarchies was significant in only one of the two female groups (K values: 0.03, $P>0.05$; and 0.51, $P<0.05$; Appendix 1, Tables VI-10 and VI-11). In both female groups reversals occurred 50 times more frequently than among males (mean of 5.0 per female group vs 0.1 per male group), yet the frequency of interactions was less than half (mean of 9.5 per observation hr in females vs 24.8 per observation hr in males).

Generally, linear hierarchies were stable over time, at least over 2 week intervals. Only one male in one group changed status (rose in rank) 2 weeks after the ranks were recorded.

This may have been because this male had a leg injury during the initial observations, but by the time the ranks were reassessed the injury had healed.

To check for a possible captivity effect on dominance status, the five highest ranked adult males (Appendix 1, Table VI-5) caught in 1985 were placed together in November 1986 with the five highest ranked adult males caught in 1986 (Appendix 1, Table VI-6). Note that one of the five males from 1985 was caught as an adult, the other four were juveniles in 1985. Every adult male caught 1985 dominated every adult male caught 1986 (Appendix 1, Table VI-9), suggesting that individuals with longer experience in captivity dominated those more recently caught. These two groups of adult males also illustrated the stability of dominance relationships within hierarchies of males: none of the five males from either group changed relative rank position despite different conditions and the addition of new members to the group.

Dominance Hierarchies in Groups of Five of Mixed Sex

Two to 3 hours of observation were generally ample to determine the rank of birds in hierarchies established in groups of five. Males tended to be more aggressive than females and therefore their rank status could be determined sooner than that of females. While males usually excluded each other from the food source, females often fed together, showing virtually no agonistic behaviour. Since groups of five individuals can produce linear hierarchies randomly with a probability of 0.12 (Appleby 1983), significance levels for linearity were not calculated for these groups. One reversal was found in one group in 1985 and one in 1986. In both cases the relationship became a linear hierarchy within 2 weeks and remained thus until the middle of April, when pairs were isolated from their groups. Hierarchies with all possible dyads interacting were recorded in 20 of 32 groups, all showed a K value of 1.0, hence a strongly linear hierarchy (Appleby 1983). In nine groups interactions of one dyad were missing, but the birds could be arranged linearly, with no reversals in the groups. The hierarchal arrangement of the remaining three groups with more than one noninteracting dyads are shown in Table II-1. In each of these latter cases there was no

Table II-1. Hierarchies within three groups of mixed sex in which there were two or more missing interactions. aM = adult male, jM = juvenile male, F = female. In each group, wins are presented horizontally, losses vertically.

rank	jM	aM	jM	F	F
1 jM		12	16	9	0
2 aM			9	1	0
3 jM		1		11	0
4 F					3
5 F					
number of noninteracting dyads:					3
K-value[a] :					0.4

rank	aM	F	F	jM	F
1 aM		18	0	9	1
2 F			0	14	13
3 F				2	0
4 jM					16
5 F					
number of noninteracting dyads:					3
K-value[a] :					0.6

rank	jM	aM	F	F	F
1 jM		11	14	4	3
2 aM			13	7	0
3 F				15	2
4 F	1				0
4 F				0	
number of noninteracting dyads:					2
K-value[a] :					0.7

---

[a] K-value determined according to Kendall's method in Appleby (1983)

question about the the ranks of the males, but the actual rank of two females remained unknown in two cases. Males were usually in the highest ranks, females in the lowest (Fig.II-2). A male was the alpha bird in all 32 groups of five magpies, a female was the omega bird in 29 groups (Fig.II-2).

Throughout the study no male was recorded to have changed rank relative to another male in any of the flocks of five of mixed sex. Two males, however, did change rank relative to females in the time between initial establishment of hierarchies and the middle of April (Fig.II-3). By contrast, females changed rank in 19 cases, 12 of which appeared to be in response to pair-formation (Fig.II-3). The other seven seemed to occur spontaneously, with no obvious influence of pair-formation or injury (Fig.II-3). All of these changes, however, were relative only to other females.

Dominance Relationships Between Juveniles and Adults

In the course of this study four males (three adults and one juvenile) in the groups of mixed sex died. Only the juvenile J1 (1986 south, Fig.II-2) was replaced by another juvenile of unknown rank. The loss of an adult in two pens in 1986 created two groups without an adult; this was unacceptable for a concurrent experiment and, therefore, one of the extra adults in the east pens was moved into the group lacking an adult.

In the 32 groups of magpies of mixed sex the most dominant bird was a juvenile male in significantly more cases (23) than an adult male (9) (binomial test, one-tailed, $P=0.01$). Combining all the males involved in this study, including those that were introduced into some of the groups after the death of the original male, 49 adult-juvenile dyads were formed (Table II-2), 35 of which were dominated by a juvenile and 14 by an adult male (binomial test, one-tailed, $P=0.002$, Table II-2). In the 32 replicates in the 2 years, adult males dominated juveniles mainly in the pens on the east side where high ranking adults were associated with low ranking juveniles (Fig.II-2). Yet some juveniles, that originally ranked in the lower half of the hierarchy of 10 juveniles, were able to dominate adult males ranked in the upper half of the hierarchy of 10 adult males. For example the juvenile males that

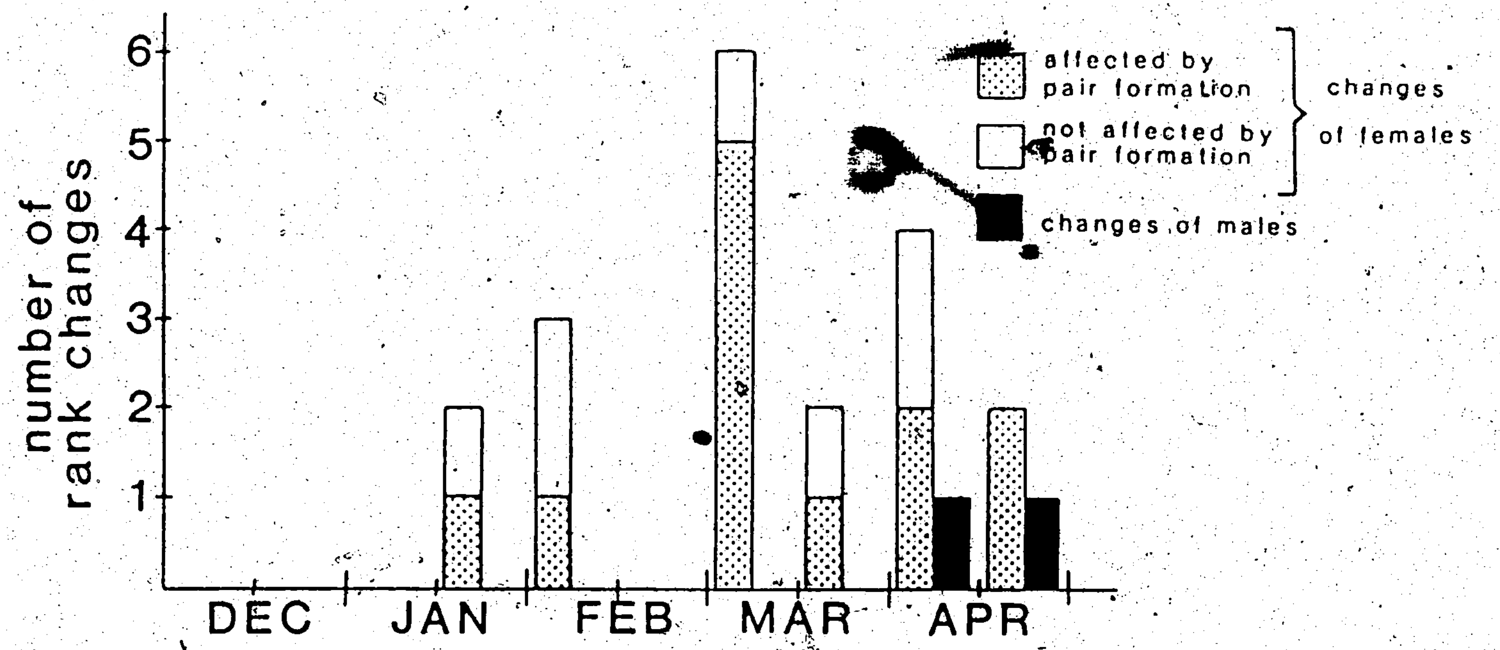

Figure II-3. Changes in rank within dominance hiearchies recorded in groups of five magpies (n = 32) of mixed sex.

Table II-2. Outcome of interactions of dyads involving adult and juvenile black-billed magpies.

Age	Alpha male in groups	Dominant bird in dyads of Males[a] alone	Females alone
Juvenile	23	35	12
Adult	9	14	5
Difference[b]	0.01	0.00	0.07

[a] based on all dyads in Fig. 2 plus five additional dyads involving birds that subsequently died and were replaced

[b] binomial probabilities, one-tailed test

originally ranked eighth, fifth, second and ninth among 10 juveniles, were able to dominate adults that originally ranked second, fifth, third and second, respectively. Of the 17 possible adult-juvenile female dyads, 12 were dominated by juveniles (binomial test, one-tailed, $P=0.072$, Table II-2).

The group of 10 adult males, which was kept from the first season to be used in the second, consisted of four birds caught in 1985 as adults (Fig.II-2: 1985 north A2, A3, A6, south A5) and six that were juveniles (Fig.II-2: 1985 north J2, J4, J5, south J1, J3, J7) during that season. All six of the latter males had dominated males caught as adults in 1985. In the second season, however, when these juveniles were adults (Fig.II-2: 1986 north A1, A2, A4, A5, A8, and A10), two (A8 and A10) of the six were subordinate to the new juveniles.

In 1986, in the north row (Fig.II-2), two adult males (A9 and A4) were able to dominate the juvenile males (J3 and J6) in the respective pens. These juveniles were ranked above a juvenile (J7) in the original group of ten, yet the latter bird ranked above an adult (A3) which ranked above A4 and A9 in the original group of 10 adults (Fig.II-2). This may indicate that location (pen) in which an adult was housed in the second year relative to that in its first year affects its dominance status, i.e. a familiar pen gives a bird an advantage in interactions with others despite the absence of its previous mate. Such, however, was not true in all cases because adult A9 and A3 were both in the same pen "held" as a "territory" the previous year. Adult A9 dominated the high ranking juvenile J3 in the same pen but adult male A3 was subordinate to low ranking juvenile J7 in its same pen. All other adult males were in different pens in each year, thus they could not be considered in this context.

DISCUSSION

Male and Female Hierarchies

Since Schjelderup-Ebbe (1922) first reported on linear "peck-right" hierarchies in domestic chickens, *Gallus gallus*, many studies have corroborated his findings (e.g. Guhl

1950; Brown 1963; Smith 1984; Rohwer 1985). Today a large body of literature on social dominance is the basis of what has become almost dogma, that dominance hierarchies in many animal species are linear. Although the use of ill-defined terms associated with social dominance can cause confusion (Deag 1977; Dewsbury 1982; Kaufmann 1983), some studies (Gwinner 1964; Baeyens 1981b; Reese 1982; Scharf 1985a), reporting linear hierarchies, have paid little attention to testing the hierarchies for linearity or stability through time, as suggested by Landau (1951), Chase (1974), Bekoff (1977) and Appleby (1983).

Recent studies using black-billed magpies have reported linear hierarchies among birds in groups of up to 31 individuals of mixed sexes (Baeyens 1981b; Reese 1982; Scharf 1985a). In all three studies, information on dominance relationships between some members of each group was lacking, none of the studies presented statistical evidence for the linearity of the hierarchies, and none presented evidence of stability of the hierarchies through time. Using the data presented in these studies, I calculated that only the hierarchy reported by Scharf (1985a) in a wild flock of mixed sex was significantly linear (Table II-3, $K=0.68$, $P<0.05$). However, if hierarchies of males were considered separately from females, then those of females failed to be significant (Table II-3, $K=0.35$, $P>0.05$). Thus, despite statements about linear hierarchies in female magpies (Baeyens 1981b; Reese 1982; Scharf 1985a), the evidence in Table II-3 suggests they have not been demonstrated. Only in this study did one of the two female groups show a hierarchy that was marginally significant. However, since reversals increase the probability of generating a linear hierarchy by chance (Appleby 1983: Table II), it is probable that a "linear" hierarchy in a group of 10 with five reversals (as was the case in the group in question) is generated by chance alone. In principal, it is possible to observe birds in captivity until interactions among all possible dyads can be recorded. Nevertheless, the frequency of interactions and the high occurence of reversals among females show not only the difference in the nature of male and female dominance relationships, but also may explain why significant linearity was not found among females in any of the field studies mentioned above.

Table II-3. Linearity of hierarchies for male and female black-billed magpies recorded in different studies.

Groups	Value	Baeyens (1981)	Reese (1982)	Scharf (1985)	this study
males	K[a]:	0.27	0.11	0.85	0.53-0.93
	n :	10	14	5	[illegible]
	p[b]:	n.s.	n.s.		<0.05
Females	K :	0.38		0.35	0.02, 0.51
	n :	4	9[c]	8	10
	p :			n.s.	n.s., <0.05
Mixed[d]	K :	0.24	n.c.	0.68	0.4-1.0
	n :	15	30	15	5
	p :	n.s.		<0.05	

[a] determined according to Kendall's method in Appleby (1983)

[b] probabilities indicated only for groups in which n>5; n.s.=not significant

[c] only two of the nine females interacted with each other

[d] males and females pooled, n.c.=not calculated, n includes birds of unknown sex

Scharf (1985a) reported hierarchies in groups of five female magpies. He based the ranking between birds on "submissive" (I suggest that the term "avoidance" would be more appropriate) behaviour to determine wins and losses at a small food source, since aggressive behaviour was often virtually lacking. The linearity of his hierarchies cannot be tested for significance because they were composed of five or fewer birds (Appleby 1983). Nevertheless, the time over which a hierarchy is stable is a good indication of its linearity (Dewsbury 1982). It is unfortunate, therefore, that Scharf (1985a) did not present data on the duration of the magpie hierarchies he studied. Consequently, the reality of their linearity must be questioned. Thus, if a hierarchy lacks linearity because the ranks of individuals change over short intervals, it is futile to attempt to correlate dominance rank with any characteristic of the individuals such as territory establishment, survival or dispersal as was suggested by Baeyens (1981b) and Eden (1987).

Baeyens (1981b) pointed out the difficulties of recording dominance rank in flocks of wild birds. Therefore, she categorized birds in the groups into three classes: high, middle and low ranking birds. Subsequently she compared the "success in establishing territories" by birds in the different categories, and found that birds in the highest ranked category did better than in the lowest one. However, only males were in the highest category and almost exclusively females in the lowest. Because magpies are monogamous, an equal number of males and females should be in possession of a territory, unless territories are established by one sex before pairs are formed, which has not been demonstrated in magpies. If more males than females occupy territories, it may be due to a different involvement of the two sexes in territory establishment as suggested by Baeyens (1981a). Females (or the lowest dominance category) in Baeyens (1981b) study may well have been present on a territory (together with their mates), but may not have been involved as actively as males in territory establishment and maintenance. Such a difference in behaviour could have accounted for Baeyens' results. The hierarchies recorded in groups of five in this study were predominantly linear when established, however, in the course of the winter the ranks of some females changed (Fig.II-3), mainly relative to other females. No male changed rank with another male. Thus, in contrast to females, male magpies establish stable, linear hierarchies with very few reversals. It seems reasonable, therefore, to suggest that the dominance hierarchy of males has some function, such as a relationship between dominance status and reproductive success (Reese 1982), but not for females.

Gwinner (1964) reported linear hierarchies in two groups of five [illegible] ravens, *Corvus corax*, however, he did state that rank changes occurred, especially [illegible] females, a situation which is also implied in Roell's (1978) study of jackdaws, *Corvus monedula*. To my knowledge, only these two studies reported that a difference in the nature of the dominance relationships between males and females similar to that in magpies. This suggests that such differences in the nature of dominance hierarchies of males and females could be a general condition, at least in corvids, and that territoriality and reproductive success can not be related to dominance relationships in both sexes equally.

Dominance Relationships Between Juvenile and Adult Males

Like Reese (1982) I found that adult males were mostly subordinate to juveniles; my results, however, contradict his prediction, based on the asymmetry hypothesis (Maynard Smith & Parker 1976; Ewald & Rohwer 1980), that adult males would be dominant in captivity. Assuming that in captivity neither foraging efficiency, nor differential levels of hunger, nor familiarity with the environment could cause asymmetries between adults and juveniles in terms of benefits gained through an agonistic encounter, one would predict rank to reflect only the fighting ability of two contestants. Reese (1982) observed that in the wild adult males won all resisted attacks by juveniles, whereas the latter resisted and won only 71% of attacks by adults. He argued that this supported the asymmetry hypothesis, because "if the expected net benefit was sufficiently large to warrant resisting an attack, adult males should win proportionately more of resisted encounters than juvenile males" (p.83). This, however, is also true for adults attacking juveniles and it is the reason why Reese predicted that adults would dominate juveniles during food shortages or in captivity. Quality of interaction other than win and loss was not recorded in this study, but resisted attacks were recorded as wins by the resister. Had adults resisted many attacks by juveniles, the outcome of many adult-juvenile dyads would have favoured adults under this rating. This was not the case, suggesting that juveniles were more aggressive or more vigorous fighters than adults. Moreover, the ranks of adult and juvenile males remained stable between November and middle of April. If the subordinate adults had wanted only to avoid conflicts in order to save energy, as suggested by Reese, why would they do this for almost 6 months, and more importantly, why would they expose themselves to open attacks by the juveniles (which in one case led to the death of the adult)?

Baeyens (1981b) and Reese (1982) showed that adult magpies were more successful than juveniles in establishing territories and producing surviving young. Yet within an age class dominant birds were more successful than subordinates in the variables mentioned above. These observations seem contradictory; adults show a higher reproductive success than juveniles, yet adults are subordinate to juveniles. If juveniles are the better fighters and hence dominant to adults, why are they not able to establish better territories and raise more young?

There are several possible ways of interpreting this apparent contradiction. One interpretation assumes that in the wild adults are also generally subordinate to juveniles, except on their territories. In the latter case the possession of space and experience probably enables them to be dominant on that space and hence to retain it. Since males establish territories near their natal site (Baeyens 1981b), males are consequently more familiar with the environment and possibly with the availability of territories as adults, than as juveniles. Møller (1982) suggested that many territories are acquired in late summer, at a time when juvenile magpies are generally still in family units, and presumably before juvenile males are attempting to occupy territories. Thus non-territorial adult males would have an advantage at this time. Magpies defend territories actively against intruders, yet stealing of mates and takeover of nests (territories) when a mate is lost can occur (Birkhead 1979; Baeyens 1981b; Møller 1982), but expulsion from territories is rarely reported. Therefore, timing of territory establishment may be the most important factor in determining which birds are successful. Since juveniles are unlikely to occupy territories at brood break up, dominance relationships between adults and juveniles would therefore have little impact on territory acquisition. On the other hand, dominance status among adults may have a large impact on overall success of the territorial cohort as found by Baeyens (1981b) and Reese(1982).

Another interpretation assumes that the dominance relationships between age classes recorded in this study are an artifact of captivity. Brown (1963) found in Steller's jays, *Cyanocitta stelleri*, and Reese (1982) in magpies that the dominance status of males decreases with increasing distance from their territories. Adult magpies in this study were captured in April and May, juveniles in September. This difference in capture timing could affect the manifestation of dominance status in captivity since adults were probably removed from their territories, whereas juveniles very likely did not have a territory at the time of capture. A comparison of dominance relationships between adults with a long history in captivity (>1 year) and adults with a short history (<1 year) suggested that the longer birds were in captivity the greater their ability to dominate others in the adult category, possibly because they had already held a "territory" in captivity from which they had not been uprooted. Such a conclusion would support the above assumption. However, if this were true one would predict that all adults in captivity more than one year would be dominant to all newly captured adults as well as juveniles. This was not the case for two of six adults which were caught as juveniles in the first season. These two juvenile males were dominant to adults in the first year, they paired, built nests, and hatched young. One can therefore assume that they accepted their pens as their territories, and that they were very familiar with the captive conditions. Despite this they were subordinate to the new juveniles in the second year. The same held true for two males that were caught as adults in 1985. These were subordinate to juveniles in the first season, however, they paired, built nests and hatched young. Nevertheless, in the second year they were again subordinate to juveniles. These cases contradict the above assumption that adults were subordinate to juveniles because they did not acclimate to the captive conditions. However, it does not contradict the assumption that adults were subordinate because they were uprooted from their territories. Most males used in both seasons were in different pens in the 2 years. They may have reacted to the change of pens as did males that were caught in the wild when removed from their territories. Only two males (Fig.II-2, 1986 north row A9 and A3) were in the same pen in the two seasons. Their dominance status was as predicted in this context in one case but not the other: male A9 was dominant to new juvenile (J3) in the second season, whereas male (A3) was subordinate to new juvenile (J7). Thus, the effect of captivity on dominance relationships between juvenile and adult males can be rejected, but the effect of uprooting males from their territories remains equivocal.

Reese (1982) reported that adults forage more often alone or in pairs, than juveniles which forage mostly in groups. This difference in sociability may be another factor influencing adult-juvenile dominance relationships under captive conditions. Adults may be more reluctant to interact with other conspecifics and prefer to live solitarily most of the time. In captivity, they were forced into association with conspecifics and once they lost an interaction they may have been unable henceforth to regain their dominance status. Such a situation would probably not hold in the wild. The significance of high aggressivness in juveniles may be related to their gregarious life style during their first winter. Because they are less efficient foragers it may be advantageous for them to live in groups (Baeyens 1981b), in which case greater aggressiveness or fighting ability may assure a male access to food in times of food shortage or enable it to establish a territory. Since solitary (or paired) adults would not have to compete with other birds to the same extent, they would not have to be as aggressive in order to have access to food.

In sum, dominance relationships between adult and juvenile male black-billed magpies, as recorded in this study and by Reese (1982), may play a minor role in territory establishment under field conditions because this event probably occurs at different times in the two age classes, and life styles, such as foraging strategy and sociability, differ in the two age classes. If true, the dominance status of birds in the two age cohorts should be considered separately when investigating survival, dispersal and reproductive success. Pooling of age as well as sex classes would yield results that are probably uninterpretable. Perhaps this is the reason why those aspects of dispersal, territory establishment, and reproductive success associated with dominance status in this species are so poorly understood.

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III. PAIR-FORMATION AND MATE CHOICE

INFLUENCE OF DOMINANCE AND AGE ON MATE CHOICE IN BLACK-BILLED MAGPIES: AN EXPERIMENTAL STUDY

ABSTRACT

The influence of age (adults of >1 year and juveniles of <1 year) and dominance status on pair-formation in captive black-billed magpies, *Pica pica*, was recorded in 32 flocks of five birds each. Adult and juvenile males of alpha dominance status paired equally frequently and more often than subordinates in these two age classes. All but one subordinate male that paired were adults. Moreover, only adult males were involved in second pair-formations (pairs that formed in flocks subsequent to the first pair-formation). Pairing success of females was independent of their dominance status, but adult females paired more often than juveniles. In choice experiments females preferred adult to juvenile males and, among adult males, dominant to subordinate individuals. Males showed no preferences for either age class of females. The choice experiments suggested that the pattern of pairing in the flocks reflected female choice. The greater pairing success of adult females may be a consequence of more intense courtship behaviour by adults than juveniles. The captive situation eliminated effects of territory quality on mate choice, but did not exclude its possible importance in mate choice in the wild.

INTRODUCTION

There are many reasons for believing that animals exert a choice when selecting a mate, as opposed to mating indiscriminately. The choice of a mate is based on the "quality" of an individual as a mating partner. Here quality includes two major groups of characteristics: those of resources held by the potential partner, and those of the potential partner itself. The mechanisms and, more importantly, the effect of mate choice on mating frequencies of "high" and "low" quality individuals have been the subject of many studies (for instance Cox & LeBoeuf 1977; Searcy 1979; Breed et al. 1980; Parker 1981; Burley 1981; Lenington 1983; Houck et al. 1985). In polygynous species with little or no male parental investment, the phenotype of the male (a reflection of its genotype) may be the most important factor in mate choice (for example "The Handicap Hypothesis": Zahavi 1975; Kodric-Brown & Brown 1984; or "The Sexy Son Hypothesis": Weatherhead & Robertson 1979, 1980; Searcy & Yasukawa 1979; Wittenberger 1981), whereas in monogamous species with equal parental investment by both sexes, the ability of a potential mate as a parent (which includes both its own attributes and the resources it holds) should be the criterion used in mate choice (Trivers 1972). Black-billed magpies, *Pica pica*, are regarded as a monogamous species with substantial parental investment by both sexes (Peitzmeier 1947; Labitte 1953; Bährmann 1963; Erpino 1968; Baeyens 1981a,b; Mugaas & King 1981). The reproductive success of magpies has been found to vary with age and sex (Baeyens 1981b; Reese 1982; Reese & Kadlec 1985), the variation being larger between age classes of males than females. Since ability as a parent varies among individuals and since investment of both parents is assumed to be essential for optimal reproductive success, one would expect both sexes of magpies to exert choice in selecting a partner (Trivers 1972). Furthermore, because reproductive success varies more among males than among females, the latter should be the more discriminating sex.

Little is known about pair-formation in magpies and virtually no information on mating preferences in this species is available. Because reproductive success is greater among adults (birds of 2 years or older) than among juveniles (1 year old birds or younger), and greater among dominant than among subordinate magpies of the same sex (Baeyens 1981b; Reese 1982), I predicted that adult birds would be preferred over juveniles and dominant birds over subordinates as mating partners. In this chapter I describe the patterns of pair-formation relative to age and dominance status in 32 captive flocks each of five magpies, as well as the results of mate choice experiments in which the chooser was exposed to a pair of stimulus birds that differed either in age and dominance status or dominance status alone.

METHODS

This study was conducted over two seasons (1985-86 and 1986-87) in a large outdoor aviary at the University of Alberta's Bioscience Animal Centre, 15 km south of Edmonton, Alberta. Between April and September 1985 and 1986, 160 magpies were captured using either circular funnel traps (Alsager et al. 1972) or nooses arranged around a decoy (Scharf 1985). The aviary is described and the general methods used in housing and marking of the birds are given in Chapter II.

Pair-Formation in Flocks

Of 32 flocks of five magpies, 12 were composed of three males and two females each and 20 of two males and three females. Each flock contained at least one adult and one juvenile male. At least one adult female was present in each of 14 flocks, whereas all 32 flocks had one or more juvenile females. This distribution was arranged in January 1986 for the first 16 flocks, and November 1986 for the second 16 flocks. In order to avoid potential preferences for birds wearing bands of a certain colour (Burley et al. 1982), all members of a flock were marked with bands of the same colours, but in different positions on the legs.

Hierarchies were allowed to develop in each of the flocks for a period of 2 weeks. Ranking of the birds in each hierarchy was done after the birds had been deprived of food over night and involved recording wins and losses over a small food source. The groups were observed from a mobile blind placed adjacent to the outside portion of the pens. Each flock was observed until at least two interactions of each bird with all the other members of its group were recorded. If, after 3 hours, a specific bird could not be assigned a rank, it was exposed individually, in the outside portion of its home pen, to each of the others in the group with the outcomes of interactions being recorded.

After the hierarchies were determined in each flock, behaviour indicating pair-formation activity (described by Baeyens 1979) was recorded weekly for 1 hour in each flock. A pair was considered to be established if on 2 consecutive weeks two birds sat next to each other with body contact, engaged in allopreening, and either searched for food or fed together.

Choice Experiments

The mate choice experiments were conducted in March and April 1987. The experimental arena was a flight cage measuring 9.8 x 3.6 x 1.9m adjacent to a 1.8 x 3.6 x 2.3m observation hut. A window of one way glass allowed unobtrusive observation of the birds in the flight cage from the hut. Opposite the hut, two wire mesh cages (each 1.3 x 1.4 x 1.0 m) were fixed in each corner of the flight cage and connected by a perch (Fig.III-1). Each cage housed one stimulus bird which was placed therein on the evening before the observations were made. Before releasing the bird making the choice, pieces of fat or meat were fixed each morning to each cage containing a stimulus bird. This induced more interactions between the bird making the choice (which had been without food overnight) and each of the two stimulus birds. Males and females were housed separately between trials which, for any given chooser, were never more frequent than every 3rd day during the experimental period (March and April). Since all birds were kept in two unisexual flocks, they knew their relative dominance status before being separated into the two small cages as stimulus birds.

On the day of observations, choosers were kept in small cages within the observation hut and released one at a time into the flight cage. Each chooser was allowed 2 minutes for acclimatization, or until it approached closer than 50 cm one of the two cages containing a stimulus bird, whichever was earlier. Subsequently, it was observed for 20 minutes. During

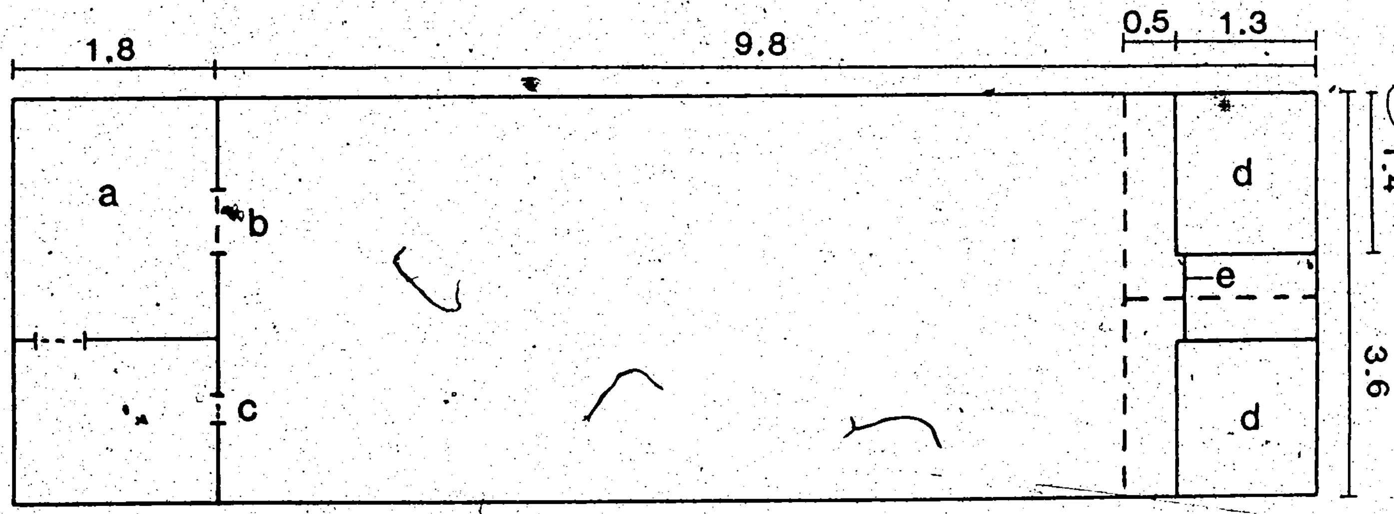

Figure III-1. Flight cage in which choice experiments were carried out (measurements in meters). a - observation hut subdivided into two smaller rooms, b - one way glass window, c - door through which choosers were released, d - cages containing stimulus birds, e - connecting perch.

this time I recorded a) the time spent by the chooser on the ground within 50 cm and/or on the connecting perch within 20 cm of a cage containing a stimulus bird, b) the number of feeding bouts of the chooser at each cage, and c) displays (of chooser and stimulus bird) such as blinking, tilting, fluffing white feathers, billing, etc. that are linked with pair-formation as described by Baeyens (1979).

I recorded a choice having been made when the chooser a) spent 1 minute or more nearer one cage than the other and if the number of feeding bouts at the same cage was greater by at least two (both requirements had to be met by the chooser in order to register a choice), or b) if courtship displays were exhibited by the chooser within 50 cm of one cage but not the other. More weight was placed upon courtship displays than the location of the chooser in deciding the nature of the choice. Thus, if the time spent and the number of feeding bouts were greater near one cage but the courtship displays were shown only at the other cage, the choice was recorded for the latter. If the chooser displayed near both cages, then no choice was recorded for the trial, irrespective of the time spent near each cage (see Appendix 2 for further details).

EXPERIMENT 1: Female Choice Between Juvenile and Adult Males

Nine adult and 11 juvenile females were given a choice between an adult and a juvenile male. Each of these 20 females was exposed to three pairs of males. One pair of stimulus males was used twice, switching their positions between the right and left cages (hereinafter referred to as the control stimulus pair). One pair of males comprised a dominant adult and a subordinate juvenile, the other two (including the control stimulus pair) included a subordinate adult and a dominant juvenile. Thus, each female was allowed to choose four times between an adult and a juvenile male, twice the adult was in the right cage and twice in the left. Three times the adult male was subordinate to the juvenile, once the adult was dominant.

EXPERIMENT 2: Female Choice Between Dominant and Subordinate Males

The same 20 females were given a choice between different dominant and subordinate males from only one age class: adult. Each female was exposed to three pairs of males, one pair being a control stimulus pair. Thus, each female was given four opportunities to choose between a dominant and a subordinate adult male. Twice the dominant male was in the right cage and twice in the left.

EXPERIMENT 3: Male Choice Between Juvenile and Adult Females

Six adult and seven juvenile males were given the opportunity to choose four times between an adult and a juvenile female (three pairs of females, one pair being used as a control stimulus pair). Twice the adult female was in the right cage and twice in the left.

RESULTS

Pair-Formation in Flocks

Pair-Formation with Respect to Dominance Status

Because there were never more than three individuals of the same sex in each group, three dominance categories were recorded for each sex separately. Alpha males and females were the highest ranked birds, omega males and females were the lowest ranked birds within each sex in each group. When there were three birds of the same sex in a flock, the second ranked bird was assigned to an "intermediate" category.

One of the 32 flocks studied was not considered in the analysis because a juvenile male died before a pair-bond between it and a juvenile female could be confirmed. In the remaining 31 flocks an initial pair of birds was recognized in 29, eight in February, 13 in March and eight in April. Considering only dominance status, alpha males (22 of 31) paired significantly more often than intermediate males (2 of 12) and omega males (5 of 31) (based on a three-way contingency table: $G=28.4$, $df=2$, $P<0.001$; Table III-1 and Fig.III-2). Age also affected pairing success of males since in each dominance category a higher percentage of adult than juvenile males paired ($G=4.9$, $df=1$, $P=0.027$; Table III-1). The only flock in

Table III-1. Pairing in male black-billed magpies relative to their dominance status and age.

Variable	Alpha			Intermediate			Omega		
	juv[a]	ad[b]	total	juv	ad	total	juv	ad	total
Paired	14	8	22	1	1	2	0	5	5
Not paired	8	1	9	6	4	10	10	16	26
Percent paired	64	89	71	14	20	17	0	24	16

[a] Juvenile males [b] Adult males

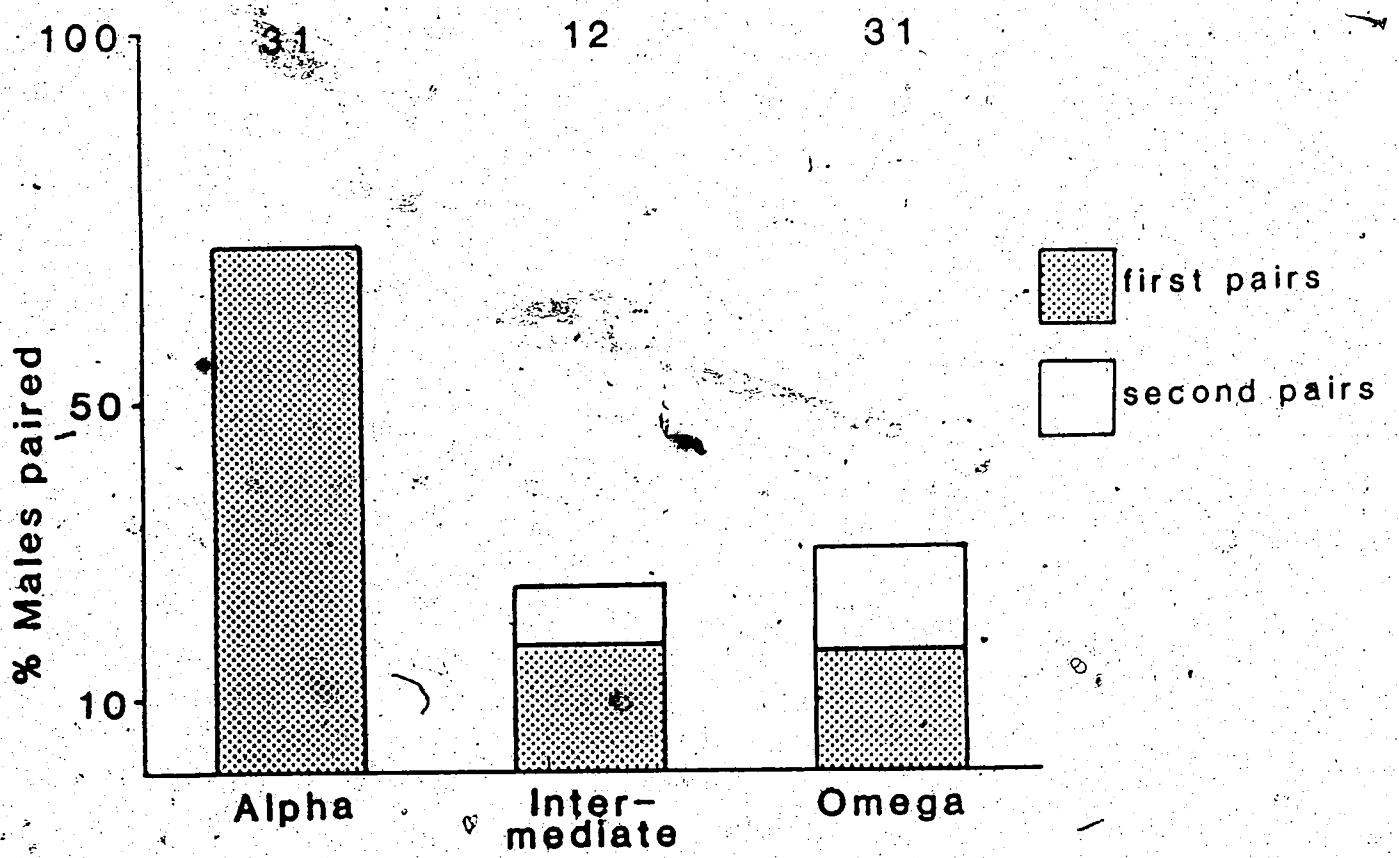

Figure III-2. Frequency with which male black-billed magpies in the three dominance categories paired. Number of birds in each category shown above histogram.

which the adult alpha male did not pair was one in which no pair-formation was recorded. By contrast, in six flocks in which the juvenile alpha male did not pair, a subordinate adult male paired instead. Females showed no significant difference ($\chi^2=2.09$, $P=0.35$) in the frequencies of pair-formation between the three dominance categories (Fig.III-3: alpha = 10 of 31; intermediate = 5 of 19; omega = 14 of 31).

Pair-Formation with Respect to Age

Overall, adult males (19 of 35) did not pair more often than juvenile males (15 of 39) (Fig.III-4; $\chi^2=1.86$, $P=0.17$), but among females, adults (13 of 15) paired more often than juveniles (21 of 66) (Fig.III-4; $\chi^2=15.1$, $P<0.001$). Frequency of pairing by juvenile males and juvenile females did not differ significantly (Fig.III-4; $\chi^2=0.48$, $P=0.49$), but adult females paired significantly more often than adult males (Fig.III-4; $\chi^2=4.78$, $P=0.03$). Overall, adults (32 of 50) paired significantly more often than juveniles (36 of 105) (Fig.III-4; $\chi^2=12.15$, $P<0.001$).

In five flocks a second pair was recorded after the establishment of the first pair. Among males, only adults were involved in these second pair-formations. If all the theoretically possible second pairs were considered, adult males paired more often in second pairs (5 of 19) than juvenile males (0 of 22) ($\chi^2=4.4$, $P=0.036$). Among the females involved in second pair-formations, adults (2 of 5) did not pair more often than juveniles (3 of 43) ($\chi^2=1.4$, $P=0.24$).

Composition of Pairs

Alpha males did not pair more often with a female from one dominance class than another (Table III-2; $\chi^2=2.67$, $P=0.26$). The composition of the other pairs, with respect to dominance status, was not analyzed statistically because sample sizes were too small (Table III-2). Pairs consisting of two adults were more frequent than any other pair composition with respect to age (Fig.III-5; $\chi^2=9.71$, $P=0.02$).

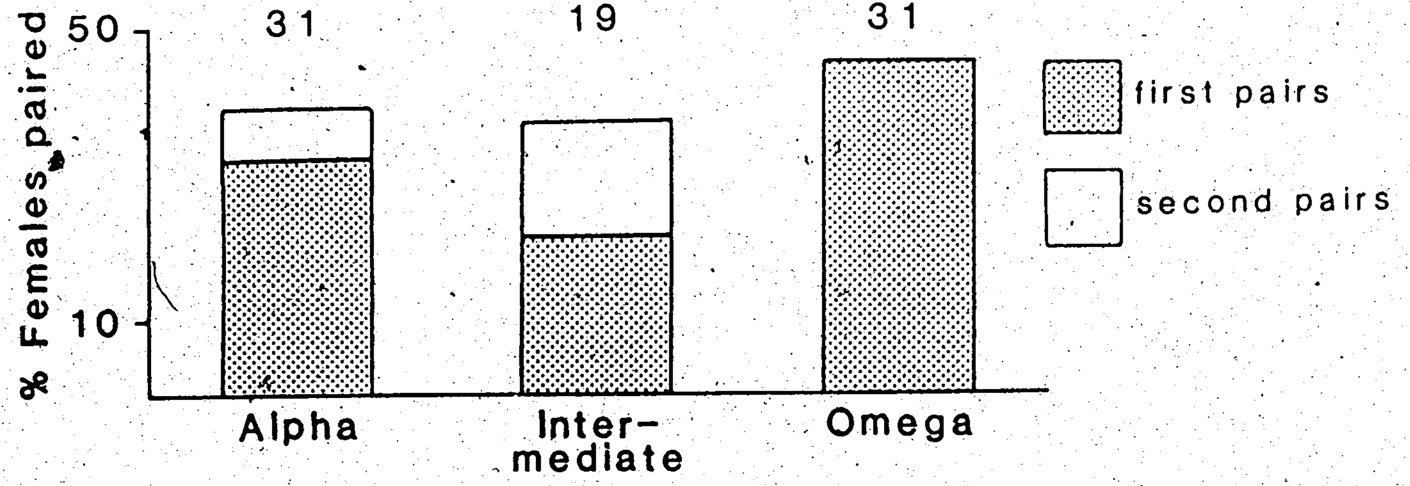

Figure III-3. Frequency with which female black-billed magpies in the three dominance categories paired. Number of birds in each category shown above histogram.

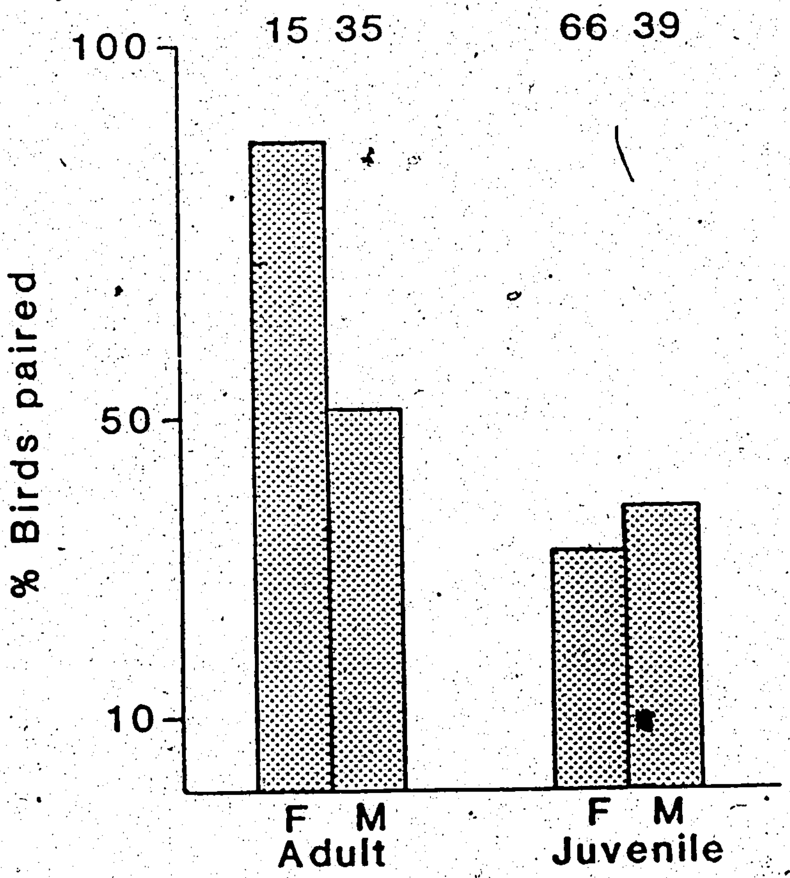

Figure III-4. Frequency with which black-billed magpies paired relative to age and sex classes. F - females, M - males. Number of birds in each category shown above histogram.

Table III-2. Pair compositions according to dominance status of black-billed magpies.

		Dominance status of famales		
		Alpha	Intermediate	Omega
Dominance status of males	Alpha	7 (22.6)[a]	2 (10.5)	11 (35.5)
	Intermediate	1 (9.1)	0	1 (9.1)
	Omega	2 (6.5)	2 (10.5)	2 (6.5)

[a] Values in parenthesis are percentage of total possible in each combination.

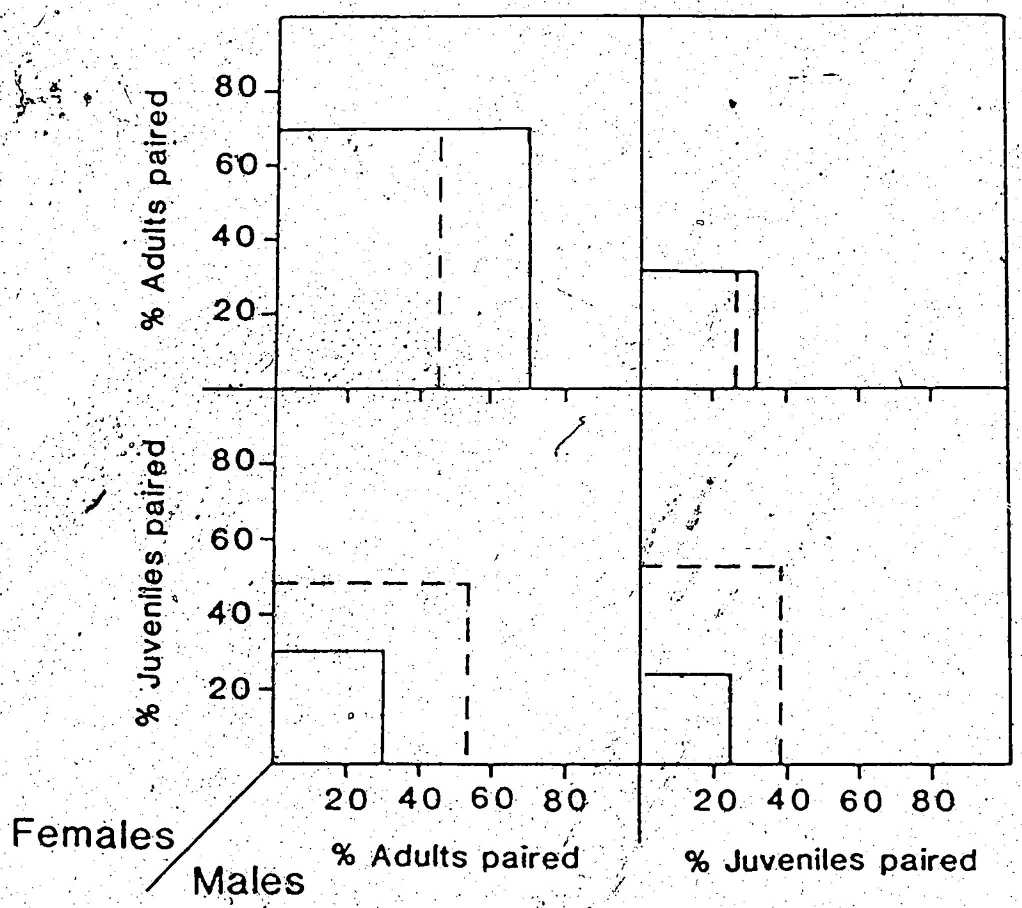

Figure III-5. Pair composition according to age classes of black-billed magpies. Solid line - percent of pairs formed from all possible pairs of a given pair composition. Dotted line - percent of paired individuals from all paired birds in any given age and sex class.

Choice Experiments

Experiment 1: Female Choice Between Juvenile and Adult Males

Three females (two adults and one juvenile) that seemed to prefer one side of the flight pen, irrespective of the stimulus males within the cages, were excluded from the analysis of mate choice. In addition, one juvenile female died after three trials leaving 16 females, each of which chose four times and one female that chose three times giving a total of 67 trials.

Females of both age classes preferred adult to juveniles males (Table III-3). In those trials in which the juvenile stimulus male was dominant to the adult, females still preferred the adult (26:9, binomial test, one-tailed $P=0.003$). There was no difference between the age classes of females in the choice of adult males (Table III-3). Adult females did not choose either adult or juvenile male more often than juvenile females did (Table III-3). In those trials in which only one male displayed (n=26), the displaying male was chosen in 61% of the trials, the other male in 7%, and neither male in 32%.

Experiment 2: Female Choice Between Dominant and Subordinate Males

One adult female showed a constant preference for one side of the flight pen and was therefore excluded from the analysis, leaving the results from a total of 76 trials. Females of both age groups preferred dominant to subordinate males (Table III-4). There was no difference between the age classes of females in the choice of dominant males (Table III-4). There was also no difference between the two age classes of females in the numbers that failed to make a choice (Table III-4). In those trials in which one male displayed (n=39), the displaying male was chosen in 85% of the trials, the other male in 2%, and neither male in 13%.

Experiment 3: Male Choice Between Juvenile and Adult Females

One juvenile male was excluded from the analysis because it showed a constant preference for one side of the flight pen irrespective of the stimulus females within the cages.

Table III-3. Mate choice in black-billed magpies: the number of times adult and juvenile females chose adult and juvenile males.

Male	Chooser females			Difference[b]
Chosen	Adult	Juvenile	Total	
Adult	16	21	37	P=0.95
Juvenile	4	5	9	
Difference[a] P:	0.006	0.001	<0.001	
Total of choices	20	26	46	P=0.68
Neither	8	13	21	
Total of trials	28	39	67	

[a] Based on binomial test, one-tailed probability

[b] Based on χ^2 (with Yates correction, where appropriate)

Table III-4. Mate choice in black-billed magpies: the number of times adult and juvenile females chose between dominant and subordinate adult males.

Male	Chooser	Females		Difference[b]
Chosen	Adult	Juvenile	Total	
Dominant	26	35	61	P=0.87
Subordinate	1	3	4	
Difference[a] P:	<0.001	<0.001	<0.001	
Total of choices	27	38	65	P=0.81
Neither	5	6	11	
Total of trials	32	44	76	

[a] Based on the binomial test, one-tailed probability

[b] Based on X^2 (with Yates correction, where appropriate)

Because of injury, an adult and a juvenile male had to be excluded from the experiments after three trials had been carried out with each of them. Therefore, only 46 trials were analysed. Males in neither age group showed a preference for one age class of females over the other (Table III-5). There was also no difference between the two age classes of males in the number of trials for which no choice was recorded (Table III-5). Seven of 21 males showing no choice were recorded as such because they exhibited courtship behaviour with both stimulus females. In those trials in which only one female displayed (n=16), the displaying female was chosen in 44% of the trials, the other female in 6%, and neither in 50%.

Differences in Behaviour of Choosers and Stimulus Birds

The number and intensity of displays of both the choosers and the stimulus birds were recorded during the experiments. Because only the number of displays and not the outcome of the choices were used in this analysis, all trials, including those in which choosers showed side preferences were included. When choosers, females displayed more courtship behaviour than males (females: 66% (105 of 159 trials); males: 40% (20 of 50 trials); $x^2=14.2$, $P<0.001$). Of the 66 trials (Experiment 1 and 2) during which stimulus males displayed, only in one (1.5%) did both males display simultaneously. By contrast, of the 27 trials (Experiment 3) during which stimulus females displayed, in 11 (40.7%) both females displayed simultaniously, a proportion that was significantly greater ($x^2=26.2$, $P<0.001$).

In Experiment 1, adult males did not display more often than juveniles (adult in 16 trials, juvenile in 10; binomial test, two-tailed $P=0.33$). In trials where the juvenile male was dominant over the adult, the number of displaying males was also not different in the two age groups (adult in 9 trials, juvenile in 7; binomial test, two tailed $P=0.80$). In Experiment 2, in which all the males were adult, none of the subordinate males displayed, whereas the dominant males displayed in all 39 trials in which one male displayed.

Table III-5. Mate choice in black-billed magpies: the number of times adult and juvenile males chose adult and juvenile females.

Female	Chooser males			Difference[b]
chosen	Adult	Juvenile	Total	
Adult	6	9	15	P=1.0
Juvenile	4	6	10	
Difference[a] P:	0.38	0.30	0.21	
Total of choices	10	15	25	P=0.14
Neither	13	8	21	
Total of trials	23	23	46	

[a] Based on binomial test, one-tailed probability

[b] Based on X^2 (with Yates correction, where appropriate)

DISCUSSION

The timing of pair-formation in the black-billed magpie is poorly documented. In this study of 160 captive magpies, establishment of pair-bonds, based on observations in February, March and April, peaked in March. However, since many birds were observed to pair in February as well as in April, the possibility that pair-formation occurs in January or even in late autumn of the previous year can not be excluded. Furthermore, some pair-formations, first detected in March and April, could have occurred earlier because paired birds may not have displayed the requisite behaviour to confirm pair-formation during the time they were observed.

The recording of mate choice in animals depends greatly on the criteria used in deciding that a choice has been made. The time spent near the object of choice has often been used in mate choice experiments (Burley et al. 1982; Bateson 1983). This method yields objective results, however, their biological meaning must then be interpreted subjectively. Recording behaviour (Cox & LeBoeuf 1977; Lenington 1983), on the other hand, probably describes the chooser's preference more adequately than just the time spent close by. This method, however, is also not free from subjective interpretations. In this study a combination of these two approaches was used to analyse the outcome of the choice experiments; more weight was put on courtship displays, while time spent nearby and the number of feeding bouts at a particular cage were used only in cases for which no courtship displays were recorded. In Appendix 2, I compared the outcome of the choice experiments using the two different methods independently and showed that results, although slightly different, led to the same conclusions.

Paired Males

In the flocks of mixed sex it was mainly (71%) the alpha males that paired. If a male other than the alpha male paired in such flocks, it was an adult in virtually all cases (92%). This pairing pattern could have resulted from female choice or male competition. Assuming it were male competition and that males mated monogamously, one would expect alpha males to prevent subordinates from pairing first and hence the latter would be involved only in second pair-formations. One would also expect the subordinate adult and juvenile males to pair equally frequently in the formation of second pairs, because both age groups of males were represented in the lower dominance categories. Neither of these expectations was supported by the data. Only adult males were involved in second pair-formations, and subordinate males that paired were almost exclusively adults. Only one juvenile, subordinate to another juvenile but dominant to an adult male, was involved in a second pair-formation. The argument that some alpha males did not pair because they were not interested in the females does not seem to hold because such alpha males repeatedly courted some females which, however, persistently avoided them. This suggests that the pattern of male pairing in the flocks is mainly a result of female choice and that females prefer adults over juveniles and dominants over subordinates. This conclusion is supported by the results of the mate choice experiments, which showed a clear preference by females for adult over juvenile males and for dominant over subordinate among the adult males. The choice by females of dominants over subordinates among adult males was a strikingly clearer result than the choice of adults over juveniles. The main reason for this difference may be that both dominance status and age varied in Experiment 1, presumably enabling females to take into account both attributes when making a chöice. The fact that females chose an adult more often, even in cases in which the juvenile was dominant, suggests that age of males is a more important determinant of female choice than dominance status.

In Experiment 1 both adult and juvenile males displayed courtship behaviour, whether dominant or subordinate. In Experiment 2, however, only the dominant males displayed. This suggests that dominant birds are able to suppress courtship behaviour in subordinates of the same age group when they are in visual contact, as in these experiments. Dominant male ravens, *Corvus corax*, have been found to suppress the courtship behaviour of subordinate males (Gwinner 1964). On the other hand, juveniles that dominated adults in the present study were apparently unable to suppress courtship behaviour in the adults. These observations suggest that dominance relationships within but not between age groups of males may be important in the reproductive biology of magpies. In Chapter II, I showed that most juvenile male magpies were dominant to adults between November and April, but suggested that this dominance relationship is of little importance in the reproductive biology of magpies, because of the different life styles in the two age cohorts; adults are more solitary than juveniles and they probably establish territories at different times of the year. Results reported herein support this suggestion.

Female magpies may prefer dominant adult males because pairs with an adult male initiate their clutches earlier than with a juvenile male (Reese 1982; see also Chapter IV), possibly because of a difference in the timing of gonadal maturation in the two age classes (Erpino 1969). Since fledging success is inversely correlated with timing of clutch initiation (Reese 1982; Hochachka 1985), pairs with adult males tend to have a higher reproductive success than pairs with juvenile males (Reese 1982). Moreover, dominant males within a given age group have been shown to have a higher reproductive success than subordinates because they are reported to establish territories of better quality and fledge more young (Baeyens 1981b; Reese 1982).

Burley & Moran (1979) showed that breeding experience of pigeons, *Columba livia*, influenced the outcome of choice by both stimulus birds and choosers. In this study, among adults two females had no breeding experience, whereas five females and one male did. The previous experience of two females and five males was not known, since they were caught as adults. Because of these small sample sizes, the question of the influence of breeding experience on mate choice in magpies could not be addressed.

Paired Females

Dominance status of females, in contrast to that of males, had no bearing on their pairing success. This difference in pairing patterns between males and females can be explained by the difference in the nature of the dominance relationships among individuals of the two sexes. In Chapter II, I showed that male magpies established stable linear hierarchies, whereas hierarchies among females were not linear and rank changes occurred frequently. It is, therefore, not surprising that dominance status of females is not a predictor of female pairing success.

Age, however, influenced success in pairing of females in flocks; adult females paired more often than juvenile females. As with males, two possible mechanisms could produce this result: competition among females, and male preference of adult females. Females in the flocks were not observed to exclude each other from the presence of males. In addition, courtship behaviour by females was very rarely observed in the flocks and begging, as described by Baeyens (1979), was not seen until females initiated incubation. This would suggest that the role of females in pair-formation is passive, and that female competition for males does not exist. Hence, one might suspect that adult females pair more often as a result of male choice. Choice experiments, however, showed that males do not discriminate between adult and juvenile females, presumably because age of females does not seem to have a great impact on reproductive success of magpies (Reese & Kadlec 1985). Because the influence of both age and dominance status on reproductive success is large in males but small in females, males have a narrower range of mate quality to choose from and thus their need to be selective is greatly diminished.

In contrast to the situation in flocks, in which female courtship behaviour was rarely seen, in the choice-experiments females appeared to be overtly the more active sex since they displayed courtship behaviour more often than males. Also, both female stimulus birds often displayed simultaneously, seemingly attempting to attract the male's attention. Although the sample size of displaying females in the choice experiments was small, it suggested that courtship behaviour of females may influence male choice, because when females displayed, it was the displaying female that was most often chosen by the male. If females are able to influence male choice, then adult females in flocks paired more often possibly because they were more active in courting males, than juvenile females, although such behaviour was seldom detected during the weekly observations. Thus, males may not discriminate between age classes of females, but may choose females that are apparently more willing to pair.

The male choice experiments were conducted in the second half of April. Had they been conducted earlier, their outcome might have been different because adult females may have shown interest in pairing earlier than juvenile females if there is a difference in the timing of gonadal maturation, as Erpino reported for males (1969). If this were the case, one would expect males to choose adult females when given the choice between adult and juvenile females in February or the beginning of March, as opposed to the second half of April.

General Discussion and Conclusion

The most frequent pair composition with respect to age was of two adults. This may be a consequence of female preference for adult males on the one hand and a result of differences in the motivation to pair between adult and juvenile females on the other. In contrast to age, dominance status affected the pairing frequencies of males but not of females. As a result, alpha males paired equally often with females from each of the dominance categories. This outcome was predicted because dominance hierarchies of females are weakly developed (Chapter II). However, this result does not agree with Lorenz' (1931) report that pairs of corvids consist mainly of dominant males and subordinate females. The prediction from his report would be that subordinate males and dominant females seldom pair. This seemed to be true for males in this study, however, it was not true for females. Roëll (1979) expanded upon Lorenz' (1931) findings by reporting that the dominance status of female jackdaws, *Corvus monedula*, depended upon the rank of males. This supports the above suggestion that the rank of males, but not of females, is important in the success of pair-formation.

Alatalo et al. (1986) found that for collared flycatchers, *Ficedula albicollis*, territory quality was the most important cue used in mate choice and that females did not prefer older males to younger ones. Also, Searcy and Yasukawa (1983) argued that high quality territories were probably the best explanation of the higher mating success recorded for older male red-winged blackbirds, *Agelaius phoeniceus*. In the present study territory quality was excluded as a possible choice criterion for female magpies. Nevertheless, females preferred older males. This may support Weatherhead's (1984) suggestions that females prefer older males because of their assumed higher genetic quality. However, there is evidence that older male magpies invest more in parental care than yearling males (Chapter IV). Thus, paternal care, the result of experience, may be more important than genetic quality. Territory quality, on the other hand, could be a consequence of male age and an additional choice criterion for females in the wild. It is not known, however, if magpies pair prior to establishing territories as, for example, in canvasbacks, *Aythya valisineria*, (Anderson 1985), or if males acquire territories before they acquire a mate, as, for example, in Middendorf's grasshopper warbler, *Locustella ochotensis* (Nagata 1986). In the former case territory quality as a criterion for choice would not come into play.

In general, the results of this study confirm the hypothesis that females are choosier than males, preferring dominant adult males. In the wild, the birds that breed are also mostly adults and within age groups they are mostly dominant birds (Baeyens 1981b; Reese 1982). However, the time and mechanisms of pair-formation in the wild are not known. Factors which may be the consequence of dominance and age, such as the quality of the territory held, breeding experience, and intensity of courtship behaviour may also be important in mate choice and success of pairing (Yasukawa 1981). Nagata (1986) reports that female grasshopper warblers prefer males with larger territories. The quality of a territory in magpies may be a function of dominance status and age because adult males and dominant males within a given age group are the more successful birds in establishing territories (Baeyens 1981b, Reese 1982). Therefore, one can assume that dominance and age influence not only territory establishment but also priority in choice of territory; i.e. adult and dominant birds occupy territories of better quality. Lenington (1980) showed that female red-winged blackbirds also preferred males holding those territories where past reproductive success had been high. She points out, however, that female choice was not always optimal. Arnold (1983) supports this finding by arguing that since mate choice is frequency dependent, it may not always be adaptive. Patterns of mate preferences may therefore differ in different populations with different sex and age ratios. More information on the mechanisms of pair-formation in wild magpies is needed to test parameters of mate quality other than those investigated in this study.

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IV. PARENTAL QUALITY

THE REPRODUCTIVE PERFORMANCE OF BLACK-BILLED MAGPIES: IS IT RELATED TO MATE CHOICE ?

ABSTRACT

Aspects of reproductive performance were investigated in 26 breeding pairs of captive black-billed magpies, *Pica pica.* Pairs with adult males constructed nests faster, initiated clutches earlier and produced larger clutches than pairs with juvenile males. There were no differences in these variables between pairs with adult and juvenile females. These findings suggest that males vary more with age in reproductive output than females. Hence, females have a greater variation of paternal quality to consider when choosing a mate. This may explain why females are more discriminant than males in mate choice (Chapter III). Paternal quality of breeding males was tested experimentally. During incubation, adult males searched longer for food, approached a potential predator closer, and attacked a territory intruder more often than did juvenile males. This suggests that adult males invest more in parental care than juvenile males. This may also be a reason for female preference of adult males (Chapter III). There were no differences in the above variables between dominance classes of males in either age group. However, since competition among individuals was excluded by the captive situation, the significance of dominance status was probably minimized.

INTRODUCTION

The choice of a mate is probably based on individual differences between prospective sexual partners, whenever such differences can be assessed. Individuals can differ in their physical attractiveness as mating partners (Zahavi 1975; Searcy & Yasukawa 1979; Weatherhead & Robertson 1979, 1980; Wittenberger 1981; Kodric-Brown & Brown 1984), in the potential amount of investment they can give their offspring (Trivers 1972; Burley 1977), in the quality of the resources they hold (Lenington 1980; Yasukawa 1981; Curio 1982; Nagata 1986), or in any combination of these. Whatever confers a difference among potential mates, individuals should choose those mates that promise the greatest probability of reproductive success (RS). The RS of black-billed magpies, *Pica pica*, differs between two age groups (adults: >1 yr old; and juveniles: <1 yr old), and between two dominance classes (dominants and subordinates); adults and dominants within a given age group show greater RS than juveniles and subordinates (Baeyens 1981b; Reese 1982). Based on an experimental study that excluded differences in territory quality, I showed in Chapter III that female magpies chose adult over juvenile males, and among adults, dominant over subordinate males. By contrast, males showed no preferences for females of either age class. I suggested that females showed more discrimination than males in choosing mates because RS varied more with age among males than among females (Reese & Kadlec 1985). Therefore, females could choose from a greater range in potential parental quality among males than the converse, making the outcome of female choice more critical to their RS than male choice of females to male RS. The reasons for these apparent differences in the RS of males and females were addressed in this study.

Baeyens (1981b) and Reese (1982) reported that among male magpies, adult and dominant individuals within a given age group, established territories of "better quality" than juveniles and subordinates. Högstedt (1981) argued, however, that territory quality determined RS and that age differences in males had a negligible effect on RS. Nevertheless, the possession of better quality territories by certain individuals could be used as a cue in female choice only if pair-formation followed territory acquisition. For magpies, however, it is not known whether they pair before or after territory acquisition. In fact the timing of mate choice may be unimportant in this context because both age and dominance status of males, assumed to be sufficient criteria for females to make a choice under conditions in which territory quality was held constant, may also be correlated closely with the quality of territory acquired. Thus, females prefer adult males and dominant males either because of their own attributes and/or because such males can establish (or already have established) territories of good quality. Högstedt (1980, 1981) rejected the necessity of differences between individual males in order to produce differences in RS, believing that differences in territory quality were all important. However, he did not address the question: what enables birds to hold territories of different quality. If differences in territory quality alone accounted for female discrimination among male occupants, females would have to rely on other criteria if differences in territory quality did not exist, as was the case in this study. By keeping territory quality constant, one can test the influence of age and dominance status of males on reproductive performance, and thereby determine whether these variables could provide critical cues to females evaluating the potential parental quality of males. In this study I investigated the reproductive performance (parental quality) of paired males in relation to their age and dominance status.

METHODS

This study was conducted over two seasons (1985-86 and 1986-87) in a large outdoor aviary at the University of Alberta's Bioscience Animal Centre, 15 km south of Edmonton, Alberta. Between April and September 1985 and 1986, 160 magpies were captured using either circular funnel traps (Alsager et al. 1972) or nooses arranged around a decoy magpie (Scharf 1985). In each season, dominance hierarchies were recorded in four groups of 10 males each, so that the dominance status (rank 1 to 10) was known for each of the 40 males involved. Subsequently, males and females were distributed, five to a pen, in the 16 pens of the aviary (see Chapter II for details of the aviary and the general methods used in marking the birds and determining their dominance status).

Of the 32 flocks of five magpies, 12 were composed of three males and two females and 20 of two males and three females (four males died subsequent to being distributed and were replaced by females, which produced the uneven number of pens containing two and three males). Each flock contained at least one adult and one juvenile male. Adult females were present in only [illegible] flocks, whereas all 32 flocks had juvenile females.

Behavioural Components of Reproduction

Starting in January displays indicating the formation of pairs (described by Baeyens 1979) were recorded weekly for 1 hour in each flock. A pair was considered to be established if on 2 consecutive weeks two birds sat next to each other with body contact, engaged in allopreening, and either searched for food or fed together. After a pair-formation was recorded, the remaining three birds were removed from the flock.

In January the outside part of each pen was equipped with a nest site (three conifers tied together in a triangle of less than 1 m to a side). An alternative nest site was created in the corner of each pen by fixing three conifer branches at right angles to the solid walls, 2 m above the floor of the inside sheltered portion of the pen. Twigs were scattered in the pens, and added if more were needed to complete the nest, and at the end of March each pen was provided with a dish containing wet mud which the birds used to build the bowl of the nest. At the same time hay was added in each pen for lining the nest bowls. Nest building activity was recorded weekly. A nest was considered completed when the mud bowl was lined with hay. The number of eggs in each nest was recorded daily, as well as the number of hatchlings.

Parental Investment of Males

The following experiments were conducted in the inside sheltered portion of the pens. During the experiments, the observer was visually isolated from the birds by partitions of fabric; an opening (15 x 30 cm), covered by a one way glass, allowed unobtrusive observation of the birds.

Feeding Effort

After being without food over night, the birds under observation were provided with 18 dishes (10 cm diameter x 7 cm deep), placed on the floor of the cage, that contained shredded newspaper, similar to the system used by Krebs et al. (1972). Three (16%) of the dishes contained 10 pellets each of dry dog food (the normal diet of the captive birds) hidden among the newspaper pieces. The number of visits by the male to each dish and the time spent searching in each dish were recorded over a period of 60 minutes. This experiment was conducted for each breeding pair on day 10 and day 15 after clutch initiation, that is during mid and late incubation.

Nest Defense

The response of male magpies to a potential predator was measured by exposing them to a domestic cat. The cat, kept in a cage of 50 cm diameter, was placed on the floor of the pen 150 cm from the base of the nest trees (or nest corner). The time spent within 150 cm of the caged cat, and the time spent uttering the harsh note (Baeyens 1979) were recorded during the first 15 minutes of exposure. This experiment was conducted for each breeding pair 2 days after the last feeding experiment (day 17).

Territorial Defense

Territorial defense was measured by exposing each pair to a captive adult male magpie. This bird, kept in a cage of 50 cm diameter, was placed on the floor of the pen, also at a distance of 150 cm from the base of the nest trees (or nest corner). The time spent within 150 cm of the "intruding" male, the number of times the cage was contacted, and the number of attempted attacks on the caged bird by the "territory owner" were recorded during the first 20 minutes post exposure. An attack was distinguished from a contact in the following way: attacks involved the "territory owner" clinging to the side walls or the roof of the cage containing the "intruder" and pecking at the wire mesh. All other ways of touching the cage were recorded merely as contacts. This experiment was conducted for each breeding pair 3 days after the last feeding experiment (day 18).

RESULTS

There where no significant differences between years in the variables recorded, permitting the data to be pooled for the analyses. Pair-formation was recorded in 29 of the 32 flocks but only those pairs (26) that completed all stages from pair-formation to incubation were considered in the analysis (Table IV-1). This sample size for variables other than clutch size was reduced to 24 (Table IV-1) because of the loss of a nest through wind blow down in one case, and disturbance in another.

Behavioural Components of Reproduction

Age Groups

Adults (>1 year old) and juveniles (<1 year old) of both sexes did not differ in the mean time of pair-formation (Table IV-1, Fig.IV-1). There was considerable overlap among pairs between nest-building activity and pair-formation (Fig.IV-1). Juvenile males started to build nests earlier than adult males but the latter completed their nests earlier; this resulted in a highly significant difference in the time needed for nest construction, adults building faster than juveniles (Table IV-1, Fig.IV-1). There were no differences in nest building activities between adult and juvenile females (Table IV-1). Females paired with adult males initiated clutches earlier and produced larger clutches than did those paired with juvenile males (Table IV-1, Fig.IV-1). Adult and juvenile females did not differ in the time of clutch initiation (Table IV-1) but adult females tended to produce larger clutches than juveniles (Table IV-1).

Dominance Classes

The extent to which dominance status was correlated with the above variables was investigated only in males because females failed to show linear hierarchies (Chapter II). Spearman rank correlation coefficients between these variables in the reproductive cycle and known dominance rank of males in groups of ten birds were calculated. Since the highest

Table IV-1. Timing of events in the reproductive cycle, plus clutch size of captive black-billed magpies. Values are presented as $\overline{x} \pm$ s.d. (n).

Variable	Adult	Juvenile	Probability
Males			
Pair formation	Mar 24±22 ~~(12)~~	Mar 14±22 (12)	0.27^a
Nest construction			
Onset	Mar 20±24 (12)	Feb 26±25 (12)	0.03^a
Duration	37.5±18.8d(12)	67.3±26.8d(12)	0.005^a
Clutch			
Initiation	May 4±8 (12)	May 13±9 (12)	0.03^a
Size	6.3±0.96 (13)	5.0±1.91 (13)	0.05^b
Females			
Pair Formation	Mar 18±26 (11)	Mar 18±18 (13)	0.94^a
Nest construction			
Onset	Mar 4±26 (11)	Mar 11±28 (13)	0.56^a
Duration	52.6±32.1d(11)	49.6±25.6d(13)	0.60^a
Clutch			
Initiation	Mar 5±10 (11)	Mar 11±9 (13)	0.18^a
Size	6.3±1.54 (12)	5.2±1.6 (14)	0.07^b

[a] Based on t-test

[b] Based on Mann-Whitney U-test

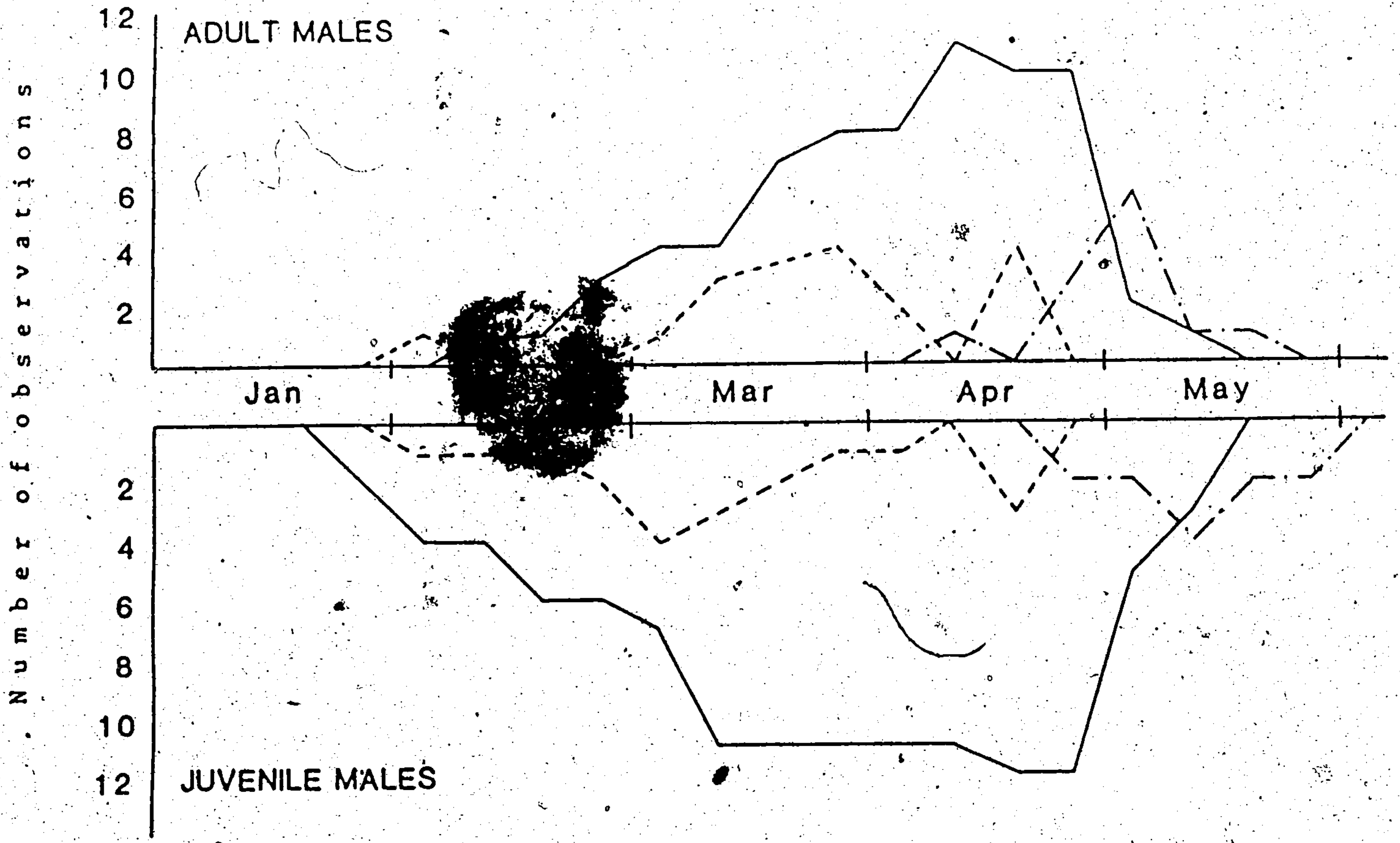

Figure-IV-1. Comparison of reproductive performance in adult and juvenile males. Solid line: number of nests under construction; dashed line: number of pair- formations recorded; dash-and-dot line: number of pairs initiating clutches.

correlation coefficient was 0.43 (non significant), dominance ranks were merged into two dominance classes for each age group and subsequently examined for differences. These dominance classes were so arranged that the sample size was the same in each. For adult males the higher dominance class consisted of birds ranked 1 and 2 and the lower class contained ranks 3 to 6. For juvenile males the higher class consisted of males ranked 1 to 3 and the lower class contained ranks 4 to 7. There were no breeding males that ranked lower than 6 among adults and 7 among juveniles. There was no difference in the time of pair-formation, onset of nest building, date of nest completion and clutch initiation, and clutch size between the two dominance classes in each age group (Table IV-2).

Parental Investment of Males

Feeding Effort

The results of the feeding experiments on day 10 and day 15 did not differ ($t=1.03$, $P=0.$[illegible]), hence they were pooled for the analysis. Adult males visited the dishes more often and spent more time at each dish than juveniles (Table IV-3). Consequently, adults spent more total time searching for food (Table IV-3).

Dominance classes within each age group did not differ in the time spent per dish (adult: $t=0.34$, $P=0.75$; juvenile: $t=0.41$, $P=0.69$), nor in the total time spent searching (adult: $t=0.54$, $P=0.60$, juvenile: $t=0.53$, $P=0.61$).

Nest Defense

There was no significant difference between the two age groups in the time spent uttering the harsh note in response to the presence of the cat (Table IV-4). Only adult males, however, approached the caged cat closer than 150 cm (Table IV-4).

There were no differences between the two dominance classes in each age group in the time spent uttering the harsh note (Mann-Whitney U-test; adults: $P=0.64$, juveniles: $P=0.62$). There was also no difference between adults in either dominance class, in the time spent close to the cat (Mann-Whitney U-test; $P=0.57$).

Table IV-2: Timing of events in the reproductive cycle plus clutch size of dominance classes in male black-billed magpies. Values are presented as $\bar{x}$ ± s.d. (n).

Variable	Dominant	Subordinate	Probability
Adult			
Pair formation	Mar 24±16(6)	Mar 24±28(6)	0.98[a]
Nest construction			
Onset	Mar 23±31(6)	Mar 16±13(6)	0.59[a]
Completion	Apr 27±2 (6)	Apr 24±19(6)	0.73[a]
Clutch			
Initiation	May 3±3 (6)	May 4±12(6)	0.59[a]
Size	6.7±0.8 (6)	6.1±1.1 (6)	0.25[b]
Juvenile			
Pair formation	Mar 12±24(5)	Mar 15±21(7)	0.84[a]
Nest construction			
Onset	Feb 17± 2(5)	Mar 4±26(7)	0.33[a]
Completion	May 8±15(5)	May 4±11(7)	0.59[a]
Clutch			
Initiation	May 15±11(5)	May 11±9 (7)	0.45[a]
Size	4.4±2.1 (5)	5.4±1.8 (7)	0.42[b]

[a] Based on t-test.

[b] Based on Mann-Whitney U-test.

Table IV-3. Time spent in searching for food by adult and juvenile male black-billed magpies. Values are presented as $\bar{x} \pm$ s.d. (n).

Variable	Adult	Juvenile	Probability[a]
Number of visits	91.9±61.0 (11)	33.0±45.5 (9)	0.03
Time spent per dish (sec)	7.0±3.1 (11)	3.2±[illegible].6 (9)	0.02
Total time searching (sec)	607.5±330.2 (11)	209.7±279.4 (9)	0.01

[a] Based on t-test

Table IV-4. Time spent in defense against a potential predator (domestic cat) by adult and juvenile female black-billed magpies. Values are presented as $\bar{x} \pm$ [illegible] n).

Variable	Adult	Juvenile	Probability[a]
Time of uttering harsh note (min)	8.1±5.0 (11)	6.1±5.5 (9)	0.47
Time spent (sec) closer than 150 cm	100.1±198.5 (11)	0.0 (9)	0.01

[a] Based on Mann-Whitney U-test

Territory Defense

There was no difference between adults and juveniles in the time spent closer than 150 cm to the cage containing an adult male magpie (Table IV-5). Although the mean number of contacts of the cage was more than 3 times greater by adults than juveniles, the difference was not significant statistically (Table IV-5). Only adults, however, attacked the "territory intruder" (Table IV-5).

There were no differences between the two dominance categories of either age group in the time spent closer than 150 cm to the cage (Mann-Whitney U-test; adult: $P=0.75$, juvenile: $P=0.62$), the number of contacts to the cage (Mann-Whitney U-test; adult: $P=0.78$, juvenile: $P=0.79$) and the number of attacks (Mann-Whitney U-test; adult: $P=0.53$).

DISCUSSION

The results of this study, in which age groups were compared within sexes for differences in reproductive performance, could have been influenced potentially by the age of the mate in each pair. However, the mates chosen naturally in this study produced combinations in which each age and sex was represented equally among the pairs (Table IV-6). Thus, the RS of adult males was influenced equally by adult and juvenile females; the same held true for the other three age and sex combinations.

Behavioural Components of Reproduction

The results suggested no difference in timing of pair-formation between adults and juveniles of each sex. These results, however, must be interpreted with care because many pairs could have been paired for varying periods of time before their pair-bond was detected and confirmed. Indeed, this may be why there was considerable overlap in time of pair-formation and nesting activity. Some pairs, in fact, were recorded as such only after the nest was completed and they began to behave in an overtly agonistic way towards the other three members of the flock in the pen. Such pairs produced the last small peak of

Table IV-5. Variables used in assessing territory defense by adult and juvenile male black-billed magpies. Values are presented as $\bar{x} \pm$ s.d. (n).

Variable	Adult	Juvenile	Probability[a]
Time spent (sec) closer than 150 cm	434.[illegible]±347.1 (11)	273.0±396.6 (9)	0.21
Number of contacts with cage	18.6±26.9 (11)	5.6±12.1 (9)	0.25
Number of attacks	6.9±10.8 ([illegible])	0.0 (9)	0.05

[a] Based on Mann-Whitney U-test

Table IV-6. Pair composition with respect to age. $X^2=1.39$ (Yates correction), P=0.24.

	Males Juvenile	 Adult
Females		
Juvenile	9	5
Adult	4	8

pair-formation in April (Fig.IV-1). This peak, therefore, seems to be an artifact of the observational methods. Nevertheless, since the methods were the same for both age groups, the potential error should also have been the same, assuming that overt behaviour in both age groups was similar. This mean time for pair-formation was recorded under captive conditions and may be different from that in the wild. Despite this potential it is still apparent that juveniles established pair-bonds in the same time period as adults.

The earlier start of nest construction by juvenile males (regardless of the age of their mate) is difficult to interpret. Perhaps, it reflects the normal timing of territory establishment and nest construction by juveniles. Møller (1982) suggested that territories established in late summer were occupied by adults. If juveniles establish territories in late winter, nest construction may be a response to territory acquisition. There is little evidence for either the cause or the function of the different duration of nest construction in the two male age categories. Experience may be a factor influencing this variable but the actual level of experience in nest construction was unknown for adult males because most were captured as adults of unknown previous history.

The differences between adult and juvenile males in the date of clutch initiation and clutch size are likely due to differences in the rate of development of their gonads (Erpino 1969) and consequent stimulation of their mates, possibly through courtship behaviour. Factors such as food availability and territory quality which could cause such differences were excluded in the captive situation. Females, by contrast, showed no significant differences between adults and juveniles in these two variables. However, the difference in clutch size was only marginally nonsignificant. Possibly, a larger sample size could yield a significant difference. Clutch sizes of all males and females are presented in Appendix 3.

Parental Investment by Males

Environmental conditions can influence the types and amounts of behaviour shown by birds. For example birds on better quality territories may find food more easily and suffer less predation pressure (Baeyens 1981b; Reese 1982) than birds on territories of lesser quality. It is possible that such birds spend less time foraging (Møller 1982) and devote more time to nest defense than birds in less favorable environments. To exclude such confounding factors, the experiments investigating paternal investment were also conducted in captivity where food availability and predation pressure were controlled variables.

Each of the experiments investigating paternal investment showed at least one variable with a significant difference between the two ages of males. Adults spent more time foraging, approached a potential predator more often and attacked a "territory intruder" more often than juveniles. In sum, adult males invested more parental care than juveniles, irrespective of territory quality. Females very seldom participated in these activities despite being able to do so. One apparent reason for their lesser involvement may have been that they were incubating at the time the tests were run. However, during the defense experiments females did leave the nest; they participated in uttering the harsh note and flew nervously back and forth in the pen. However, no female was recorded approaching closer than 150 cm the caged cat nor attacking the "territory intruder". This difference in male and female behaviour agrees with the observations of Baeyens (1981a) who found that males [illegible]nt more time in territory defense than females.

It can be argued, that recording paternal investment [illegible] be more conclusive if carried out while young were in the nest. Such experiments were attempted during this study, however, only three pairs fledged young successfully (see Appendix 4). Most of the young died within 10 days of hatching, probably because the available diet was inappropriate. Nevertheless, since differences between age groups of males were demonstrated for the incubation period in this study, there would seem to be no reason why these differences were not maintained throughout the nesting period. Parents may change the amount of investment they provide through different stages of the reproductive cycle (Trivers 1972; Maynard-Smith 1977; Grafen & Sibly 1978; Ridley 1978). There is no reason, however, to predict a greater change of paternal investment by juveniles than by adults. Thus, the differences shown in this study would likely have persisted into the later stages of brood care, had I been able to record them.

Parental Care and Mate Choice

The recorded observations showed that the timing of events during the early stages of the reproductive cycle vary with age in males but not in females, supporting the suggestions of Reese & Kadlec (1985). These differences may explain the differential mate choice observed by the two sexes (Chapter III); females preferred adult to juvenile males but males did not discriminate between the two age groups of females. Since females did not show differences between adults and juveniles, in the variables investigated, the outcome of mate choice would be less important for the RS of males than females. By contrast, females may maximize their own RS by choosing males which are better parents. Hochachka (1985) did not find any correlation between clutch size and RS in magpies, but Reese & Kadlec (1985) did, and both studies reported an inverse correlation between the date of clutch initiation and fledging success. Thus, males which are able to promote earlier initiation of clutches increase their probability of RS. Such males are adults, not juveniles. Moreover, in addition to being able to promote earlier initiation of clutches, adult males invested more in parental care than did juveniles (at least through incubation), adding to the former's overall better reproductive performance. Thus, in pair-formation there seem to be several reasons for females to choose adult males when they are available. The role of territory quality in mate choice can not be answered by this study. However, the suggestion that differences between males are negligible and not necessary to explain differences in RS (Högstedt 1980,1981) was not supported by this study.

Baeyens (1981b) and Møller (1982) defined territory quality in terms of the permanency of its occupancy and the success of nesting attempts in previous years. These two variables, however, are related because magpies tend to stay in the same territory over several seasons when they have bred successfully (Baeyens 1981b). The conclusion that better quality territories contain more successful pairs is therefore a circular argument. Hochachka (1985) found that fledging success was similar on a given territory in consecutive years. Because of a high turnover of breeding birds on territories between years, he concluded that this result was due to territory quality. However, despite a small sample size (n=6) he found that males that shifted territories tended to produce similar numbers of young in consecutive years. Thus, although our data combined do not reject the effect of territory quality on RS, they do emphasize the influence of parental quality on RS, as is suggested by the differences between the two age groups of males found in this study.

Weatherhead & Robertson (1979) and Weatherhead (1984) argued that the genetic contribution of male red-winged blackbirds, *Agelaius phoeniceus*, is the major factor influencing female choice and that parental quality can be excluded, mainly because males invest little parental care. This study of magpies supports the conclusions of Mugaas & King (1981) that males make a significant investment in brood care. It also showed that paternal care improved with age. Thus the sexy son hypothesis (Weatherhead & Robertson 1979) does not appear to be a viable explanation for female choice in magpies. Contrary to magpies, which show obligate monogamy (P. Dunn pers. comm.), red-winged blackbirds are polygynous. This difference in mating systems may require that different criteria be used in mate choice by the two species.

Dominance status has been reported to influence mate choice in animals (Lott 1979; Breed et al. 1980; Dewsbury 1982; Halliday 1983). I showed in Chapter III that female magpies prefer dominant to subordinate males. While Baeyens (1981b) and Reese (1982) showed that dominant males have a higher RS than subordinates, I found no differences in parental quality between dominant and subordinate males in any of the variables investigated under captive conditions. Reese (1982) suggested that subordinate individuals may have been physiologically less mature than dominant ones. If physiological maturity were responsible for such differences, one would expect to find similar results in the captive situation as well. This was not the case. Rather, the lack of influence of dominance on reproductive performance in this study was probably due to the lack of competition between individual breeding males. Dominance rank is not an intrinsic attribute of the individual, it is a relationship between two individuals (Barette & Vandal 1986), usually expressed in a competitive situation. Since each male was provided with one pen where it was protected from the interference of other males, its dominance rank could not be expressed in the variables measured in this study. In the wild, however, where competition for any limiting resource is likely to occur, dominance status may be a very important factor in gaining access to such resources and consequently enabling dominant individuals to provide better parental care. For instance, dominant birds can acquire better quality territories, as was reported by Baeyens (1981b) and Reese (1982), because they outcompete subordinates. This and presumably other advantages of high dominance status in the breeding biology of magpies may explain why females prefer dominant males (Chapter III).

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V. CONCLUDING DISCUSSION

The results of this study have shown a difference between male and female dominance hierarchies. This difference may have a wider distribution than just among magpies, at least among the Corvidae, as suggested by the studies of ravens (Gwinner 1964) and jackdaws (Roëll 1978). In both studies a higher rate of rank change among females than males was suggested; Roëll stated that a female's rank depended upon that of its mate. Female carrion crows (*Corvus corone*) seem to exhibit a similar dependence of rank on male dominance status (H. Richner pers. comm.). Unfortunately, none of these studies described the nature of hierarchies in the two sexes separately. It remains, therefore, a topic that needs further investigation in different species. However, even if such differences between male and female hierarchies exist only among magpies, one is still left with the question of the significance of such differences between males and females. In the second chapter I suggested that males may exhibit a stronger, more rigid linear hierarchy than females because the former are more active in territory establishment and maintenance (Baeyens 1981a). Also, in the third chapter, I showed that dominant males were chosen over subordinates by females, whereas females from all ranks paired equally often. All of the above factors support the suggestion that a high dominance rank is important for males but not for females. Such differences in dominance relationships can be demonstrated only in groups where complete dominance matrices are established, preferably without any missing interactions. The calculation of a dominance index (Reese 1982; Eden 1987), based on the proportion of wins per total number of interactions, provides a level of probability that such an individual will win in future interactions with other individuals, but it does not give much information about the nature of the hierarchies. The value of a dominance index is questionable in systems in which intransitive relationships exist, because an individual with a high dominance index may in fact be defeated by an individual with a low dominance index. It is a valid point, however, that in considering the relationship between dominance status and dispersal or survival, it is more likely that the probability of winning an interaction (as expressed by a dominance index) rather than an individual's exact standing in a hierarchy will determine the rate of dispersal and mortality (Eden 1987; Wiggett 1988). In this study, it was not my intention to solve the controversy between the use of a dominance index and an exact rank position in a hierarchy. I raise this point here to draw attention to the possibility of studying this problem in magpies because, now, both systems have been used in studies of this species.

The observed dominance hierarchies (Chapter II) provided evidence that juveniles dominate adults. Similar published evidence is very scarce (Watson 1970; Reese 1982), but there is some anecdotal evidence for similar dominance relationships between adults and juveniles in an Idaho population of magpies (L. Reed pers. comm.), in dark-eyed juncos, *Junco hyemalis*, (B. Holbertson pers. comm.) and American robins, *Turdus migratorius*, (D.A. Boag pers. comm.). Whether such relationships are widespread among the corvids and other passerines remains unknown. Furthermore, the significance of high dominance status of juveniles is not explained by this study. I suggest that the differences in life style between the two age groups is a possible explanation, and that the aggressiveness of juveniles has little impact on the survival and reproductive success of adults (Chapter II). This suggestion is supported in Chapter III, where I showed that females chose and paired with adults even when juveniles were dominant633urther support is evident from the paternal investment experiments (Chapter IV). A higher investment in paternal care by adults may explain the higher reproductive success of adults (Baeyens 1981b; Reese 1982), which at first seemed to be contradictory to the low dominance status of adults (Chapter II). I suggested in Chapter II that it was not the captive situation but the uprooting of adults from their territories that may have influenced the dominance relationships between juveniles and adults. Brown (1963) found in Steller's jays, *Cyanocitta stelleri*, and Reese (1982) in black-billed magpies that the farther a territorial male was from its territory, the lower was its dominance status. It would be useful to have more information on the influence of territory possession on the dominance relationships between adults and juveniles. If territorial adults were able to dominate juveniles on or near their territories throughout the year, it would mean that the dominance relationships between adults and juveniles, as found in this study and by Reese (1982), are relatively unimportant in the wild. Such relationships may be found predominantly in artificial situations such as at feeding stations and in captivity, especially, in the latter case, when all adults had been uprooted from their territories. There is data from this study, however, that showed that despite being in its home cage (territory) an adult male still was subordinate to a juvenile male. Furthermore, if adults establish territories in summer and early autumn (Møller 1982) they are more likely to possess a territory than juveniles, and hence of being influenced by the possession of a territory in any future aggressive encounters. Information on the timing of territory establishment, presently unknown, is therefore important in the context of how territory ownership influences dominance status.

Dominance status of males influences female mate choice (Chapter III), but does not seem to be, in contrast to age, a good indicator of paternal quality (Chapter IV). This raises the question: what is the significance of female preference for dominant males? If territory ownership influences dominance status, or if the latter determines the probability of territory acquisition by males, then females may use dominance status as a cue to discriminate among males. Knowledge of the timing, and the mechanism of territory establishment is critical also in this context. Whether males establish territories alone or together with their mate may be immaterial if the ability of a male to defeat others is central to success in competing for territories. On the other hand, if males acquire territories before they find a mate, and if the possession of a territory influences their dominance status, the latter may also be used as a cue by females to discriminate between males that do and do not possess a territory.

While dominance status and age influence pairing success of males, and age determines paternal care, neither dominance nor age seem to affect pairing of females (Chapter III) or maternal care (Chapter IV). Because females do not establish well determined dominance relationships (Chapter II), males could not, if they would, choose among females with respect to dominance status. This may explain the cause of the equal pairing success of all female dominance categories. However, a functional explanation for this observation could not be given by this study. Again, information on the timing of pair-formation and territory establishment is needed to answer such questions. Perhaps, females do not compete for males nor do they establish territories and, therefore, they do not need to invest time and energy in establishing and maintaining dominance hierarchies. In addition, age of females did not affect mate choice by males (Chapter III). This result may be explained by the observation that females in the two age groups did not differ in terms of the variables measured during the reproductive cycle (Chapter IV). One can therefore argue that which female they choose is not crucial for males, since both female age groups show the same reproductive output. However, in the flocks of five, adult females paired more frequently than juveniles. Was this a result of female competition or male choice? Such an explanation would be contradictory to the above arguments that females do not compete and that they do not differ in reproductive variables between the two age classes. As argued in the third chapter, males may be more discriminant at different times of the year while choosing their mate, or females may differ in their motivation to pair depending on age and maturity. In addition, in Chapter IV I showed that the difference between adult and juvenile females in clutch size was only marginally nonsignificant (see also Appendix 3). If, with a larger sample size, adult and juvenile females could be shown to differ in clutch size, this difference could be a reason for males to discriminate among females, as argued in Chapter III.

This discussion has emphasized problems and questions that have arisen from results obtained during this study. They are intended to stimulate future thought about the problems of mate choice as well as to suggest further research on this important subject. Besides theoretical problems, future work on magpies must also face practical problems, namely in trapping birds and determining their sex and age. A discussion of the latter is presented in Appendix 5.

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VI. Appendix 1

Hierarchies in Unisexual Groups of Ten Captive Black-billed Magpies

Each table shows the hierarchal arrangement of magpies in one group of 10 birds. Winners are listed vertically, losers horizontally. Asterisks indicate an "intransitive relationship" in which an individual that was displaced by a higher ranking bird was able to dominate an individual that ranked even higher than the latter. Non-interacting dyads are indicated by a zero. The K-values were derived as discussed in Chapter II; for a group of 10 individuals, a hierarchy was significantly linear when $K>0.50$.

Table VI-1. The outcome of interactions among adult male black-billed magpies. Two dyads were not recorded interacting; total number of interactions= 272. $K=0.88$; $P<0.05$.

	RRWS	WSOG	SYRO	SOWR	SGWR	RRGS	SBWR	SYRY	SGWG	SWWR
RRWS		13	12	5	2	3	6	8	5	2
WSOG			11	2	5	0	1	5	4	1
SYRO				1	2	2	1	10	2	0
SOWR					10	15	8	4	6	5
SGWR						15	10	8	10	9
RRGS							9	13	8	3
SBWR						3		8	2	1
SYRY									14	3
SGWG										5
SWWR										

Table VI-2. The outcome of interactions among adult male black-billed magpies. One dyads were not recorded interacting; total number of interactions= 218. K=0.93; P<0.05.

	-SOB	SROG	SOOB	----	SYBO	SBOB	-SOG	WWSY	SBOG	SWOG
-SOB		15	8	2	5	4	10	7	1	9
SROG			6	6	4	9	6	7	1	4
SOOB				6	4	4	3	1	0	10
----					1	3	4	1	1	2
SYBO						4	2	6	1	4
SBOB					1		9	5	4	5
-SOG		2						12	3	6
WWSY							1		8	5
SBOG										
SWOG										

Table VI-3. The outcome of interactions among juvenile male black-billed magpies. Seven dyads were not recorded interacting; total number of interactions= 229. K=0.72; P<0.05.

	SOWW	SBWB	SWOW	SOOW	SBOW	SOBB	WYGS	SGOW	SR-B	SWW-
SOWW		11	4	9	3	1	2	1	0	4
SBWB	1		3	16	13	6	13	0	3	3
SWOW				15	2	5	1	0	1	5
SOOW			1		18	21	6	6	2	8
SBOW						4	3	0	0	3
SOBB							1	6	0	11
WYGS								4	0	2
SGOW									4	6
SR-B										1
SWW-										

Table VI-4. The outcome of interactions among juvenile male black-billed magpies. Two dyads were not recorded interacting; total number of interactions= 273. K=0.89; P<0.05.

	SYRR	SBRR	SRYY	SWRR	SRRR	SOGG	SYGG	SROO	SORR	SOYY
SYRR		5	5	0	3	1	9	0	3	4
SBRR			7	7	10	3	7	2	1	1
SRYY				9	11	6	10	9	7	2
SWRR					14	3	5	7	3	3
SRRR		1				14	22	11	7	11
SOGG							2	6	2	3
SYGG						1		5	2	6
SROO									12	2
SORR										9
SOYY										

Table VI-5. The outcome of interactions among adult male black-billed magpies caught 1985. Seven dyads were not recorded interacting; total number of interactions= 251. K=0.52; P<0.05.

	OSWB	SRWY	SYBR	OSGB	SGWY	SYOB	SYGB	SWGB	SB1YO	SOYB1
OSWB		11	8	6	16	16	21	2	3	8
SRWY			5	1	6	0	4	0	0	0
SYBR				4	11	6	15	2	0	4
OSGB					7	3	7	0	1	1
SGWY						7	12	1	0	7
SYOB							10	4	5	1
SYGB								4	5	8
SWGBO						1			6	2
SB1YO			1							8
SOYB1						1				

Table VI-6. The outcome of interactions among adult male black-billed magpies caught 1986. Four dyads were not recorded interacting; total number of interactions= 269. K=0.84; P<0.05.

	YYSY	SBRR	SWWB	SB1OG	SRG YBY	SBGY	OWW SBR	BRR OWS	SRB YYY	SWRB
YYSY		5	0	6	8	8	5	10	9	10
SBRR			5	16	14	8	1	5	5	5
SWWB				3	1	1	0	1	0	2
SB1OG					6	6	4	4	4	2
SRGYBY						5	6	15	7	3
SBGY		1					12	17	12	14
OWWSBR								5	0	1
BRBOWS									8	7
SRBYYY										2
SWRB										

Table VI-7. The outcome of interactions among juvenile male black-billed magpies. Three dyads were not recorded interacting; total number of interactions= 258. K=0.93; P<0.05.

	SBOO	SBGG	SB1WW	SYWW	SWGG	SOWW	SRGG	SRBB	SWRR	SBOG
SBOO		7	1	3	2	3	2	11	2	3
SBGG			3	17	2	1	6	8	4	5
SB1WW				11	4	3	6	6	1	0
SYWW			1		7	10	12	13	17	10
SWGG			2			2	8	2	6	0
SOWW							11	8	9	1
SRGG								1	12	1
SRBB					1				5	1
SWRR										0
SBOG										

Table VI-8. The outcome of interactions among juvenile male black-billed magpies. Two dyads were not recorded interacting; total number of interactions=294. K=0.73; P<0.05.

	SWB1B1	SYWB	SBBB	SRWB	SOOD	SBBG	SGOG	SYOG	SB1WB	SBBY
SWB1B1		8	11	20	3	7	11	6	9	6
SYWB			7	7	2	7	2	7	0	3
SBBB		1		11	7	14	7	16	14	6
SRWB					2	8	11	1	1	7
SOOD						5	8	0	1	4
SBBG				1			4	2	6	3
SGOG				1				3	9	4
SYOG									4	2
SB1WB		2*		5*	1		1			3
SBBY							2			

Table VI-9. The outcome of interactions among adult male black-billed magpies. Two dyads were not recorded interacting; total number of interactions= 168. K=0.87; P<0.05.

	OSWB	SRWY	SYBR	OSGB	SGWY	YYSY	SBRR	SWWB	SB1OG	SRGYBY
OSWB		5	4	1	9	2	2	1	2	2
SRWY			7	5	3	5	4	1	2	0
SYBR				5	11	6	3	2	3	1
OSGB					9	2	5	1	1	2
SGWY						10	6	9	5	6
YYSY							5	1	5	0
SBRR								1	3	2
SWWB									2	4
SB1OG										3
SRGYBY										

Table VI-10. The outcome of interactions among juvenile female black-billed magpies. Thirty dyads were not recorded interacting; total number of interactions= 69. K=0.03; P>0.05.

	SBYY	SBOO	SWOO	S-G-	S---	SGOO	SGGG	SGYY	SWYY	SYOO
SBYY		1	2	7	6	0	1	0	0	0
SBOO			1	3	6	0	0	0	0	0
SWOO				12	3	0	0	0	0	0
S-G-					9	1	0	0	0	0
S---			7*			2	1	1	0	0
SGOO		1*	3*				0	0	0	0
SGGG			2*					0	0	0
SGYY									0	0
SWYY	1*									0
SYOO										

Table VI-11. The outcome of interactions among adult and juvenile female black-billed magpies. Twelve dyads were not recorded interacting; total number of interactions=121. K=0.51; P<0.05.

	S-RG	SR--	SB-O	SO--	RS-G	S-YG	SO-W	OS-W	SB-W	SO-G
S-RG		6	2	4	3	4	8	2	3	0
SR--	2		3	0	0	4	3	3	4	1
SB-O				3	0	3	1	0	2	2
SO--		5*			2	0	1	1	1	4
RS-G		3*	1*	1		1	0	0	2	0
S-YG				3*			7	4	2	3
SO-W		1						3	7	0
OS--			4*						0	0
SB-W										2
SO-G										

VII. Appendix 2

COMPARISON OF DIFFERENT METHODS OF ANALYSIS IN MATE CHOICE EXPERIMENTS

Establishing that a choice has been made in experiments dealing with mate choice in animals depends upon interpreting the significance of the variables recorded. Mate choice has been recorded in a number of ways, including the behaviour of choosers (Cox & LeBoeuf 1977; Burley and Moran 1979; Lenington 1983), the time spent near the object of choice (Lenington 1980; Burley et al. 1982; Bateson 1983), the rate of mating (Cox & LeBoeuf 1977; Wells 1977; Houck et al 1985), the size of harems (Clutton-Brock et al. 1979; Yasukawa 1981), and discrimination between two sources of odour (Breed et al. 1980; Lenington 1983). Despite the diversity of approaches, all these studies conform to Halliday's (1983:4) definition of mate choice as being "any pattern of behaviour, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others." Since this definition only requires that the distribution of matings be not random, it excludes the necessity of showing "true preferences" by the choosers. Halliday argued that, for selection to occur, only the distribution of mating frequencies is relevant and not the precise mechanisms involved. Therefore, in a study of mate choice it is most important to record those variables that best discribe the probability of mating frequencies, which may not be the true preferences of choosers.

Bearing this in mind, choice experiments with magpies in this study (Chapter III) were designed to record the time spent by the chooser near each stimulus bird, the number of feeding bouts and the courtship displays exhibited at each cage containing a stimulus bird. It was assumed that the time spent by the chooser close to one or the other stimulus bird would indicate the probability of mating with the latter. The number of feeding bouts was recorded because earlier it had been observed in flocks of five, that those magpies of different sex which fed together without agonistic interactions were either paired at the time or were later often recorded as pairs. It is likely courtship behaviour that best discribes the probability of mating with a given stimulus bird, since such behaviour is, by definition, mostly exhibited during pair-formation or pair-maintenance (Baeyens 1979). This was the reason why most weight was placed upon courtship behaviour in the analysis. Time spent near a stimulus bird and number of feeding bouts near it were used only in those trials in which no courtship behaviour was recorded. However, it could be argued that the intensity of courtship displays is often very variable and the decision of whether or not courtship was displayed may be subjective at times. Also, since cages containing the stimulus birds were relatively close together in this study, the possibility that the chooser displayed near one cage but addressed its behaviour to the stimulus bird in the other can not be excluded completely. Therefore, to compare the different possible approaches in analyzing the data from this study, each variable (time spent nearby, number of feeding bouts, courtship displays) was evaluated separately (Tables VII-1 to VII-3) and the outcome of each compared to that used in Chapter III (Table VII-4). Individual choosers sometimes showed side preferences in one or more of the recorded variables (three independant and one combined). When this occurred the variable concerned was discarded from the analysis in each trial. For example, in Table VII-1, adult female 1423 showed side preference when all variables were combined (All) and consequently this result was eliminated from the totals of each trial. The excluded outcomes are underlined in Tables VII-1 to VII-3.

While the distribution of frequencies of choices using each of the three variables recorded, was not the same, the conclusions drawn from the ratio of choices (by means of a binomial test) were, nevertheless, the same for each variable in all three sets of trials. Thus, whether one used only time spent nearby, or number of feeding bouts, or courtship displays or all together, the conclusion was always that females chose adult over juvenile males and dominant over subordinate adult males, and that adult males showed no preferences (see Chapter III).

Because the distribution of choices was not the same for the three variables, one is left with the question: which of the variables gives the most precise measure of choice? I suggest that, despite the reservation stated above, the recording of courtship displays is the most accurate way of describing the probability of the establishment of pair-bonds and subsequent mating because this behaviour is used by animals to form pairs. Nevertheless, the use of courtship behaviour to measure the outcome of choice also depends on the motivational state of the chooser (Halliday 1983). Thus, courtship may not always be displayed. The level

Table VII-1. Outcome of female choice between adult and juvenile male black-billed magpies. A=adult was chosen; J=juvenile was chosen; 0=no choice recorded.

	Male stimulus pairs															
Adult:	GS-0 (R)[a]				Y-OS (L)				S--G (R)				GS-0 (L)			
Juvenile:	SR-G (L)				S-OB (R)				S--Y (L)				SR-G (R)			
Chooser Band Number	T[b]	F[c]	B[d]	All	T	F	B	All	T	F	B	All	T	F	B	All
Adult females																
999	A	A	J	J	A	0	A	A	0	J	A	A	A	0	A	A
1423	A	0	0	0[e]	J	0	J	J	A	A	0	A	0	0	0	0
1121	0	0	0	0	0	A	0	0	A	A	A	A	A	A	A	A
1452	0	0	0	0	J	A	J	J	A	0	A	A	A	0	A	A
1155	A	A	0	A	J	A	A	A	A	A	0	A	A	0	A	A
789	J	J	J	J	0	J	J	J	A	A	A	A	A	0	A	A
Adult:	S--G (L)				Y-OS (R)				S--G (R)				GS-0 (L)			
Juvenile:	S--Y (R)				S-OB (L)				S--Y (L)				SR-G (R)			
498	0	J	0	0	A	A	0	A	0	A	0	0	A	J	0	0
784	A	0	A	A	J	0	0	0	J	0	J	J	A	0	A	A
1127	A	0	A	A	0	0	A	A	0	0	0	0	A	0	0	0
Total																
A	5	2	2	2	2	3	3	4	5	4	4	5	8	1	6	5
J	1	1	2	2	4	1	3	2	1	1	1	0	0	0	0	0
0	3	5	5	3	3	4	3	1	3	3	4	2	1	7	3	2
Juvenile females																
1457	A	0	A	A	A	A	0	A	A	0	0	0	J	J	A	A
1491	A	A	A	A	0	A	0	0	A	J	0	0	A	A	0	A
1439	A	0	0	0	A	A	0	A	0	0	A	A	J	J	0	J
1443	0	A	0	0	J	0	0	0	A	A	0	A	J	J	A	A
1461	A	A	A	A	A	A	0	A	A	A	A	A	0	0	0	0
1452	A	A	A	A	J	A	J	J	A	0	J	0	0	0	A	A
1426	A	0	0	0	0	0	J	J	A	A	A	A	A	0	A	A
1482	A	A	0	A	0	J	0	0	A	A	A	A	J	J	J	J
1159	J	J	0	J	J	J	0	J					A	A	0	A
1157	0	0	0	0	A	A	A	A	0	A	0	0	A	0	A	A
1493	J	J	A	A	0	A	0	0	A	A	A	A	A	J	0	0
Total																
A	7	4	5	5	4	7	1	4	8	5	5	5	5	2	5	7
J	2	2	0	1	3	1	2	3	0	1	1	0	4	4	1	1
0	2	4	6	4	4	2	8	3	2	3	4	4	2	4	5	2

[a] Side which male was placed: R=right, L=left.
[b] Time spent within 150 cm of either stimulus bird.
[c] Number of feeding bouts at either cage.
[d] Courtship displays within 150 cm of either stimulus bird.
[e] All underlined outcomes were discarded for analysis because of side preferences (see text).

Table VII-2. Outcome of female choice between dominant and subordinate adult male black-billed magpies. D=dominant male was chosen, S=subordinate male was chosen, 0=no choice recorded.

	Male Stimulus Pairs															
Dominant: Subordinate:	S--G (L)[a] Y-OS (R)				GS-O (L) SB-R (R)				OS-W (R) SG-W (L)				S--G (R) Y-OS (L)			
Chooser Band Number	T[b]	F[c]	B[d]	All	T	F	B	All	T	F	B	All	T	F	B	All
Adult females																
999	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
1423	D	D	D	D	S	D	D	D	D	S	D	D	D	0	D	0
1121	D	D	D	D	0	D	D	D	S	S	D	D	D	0	D	D
1152	0	D	D	D	D	D	D	D	D	D	D	D	D	S	D	D
1155	D	D	D	D	D	D	0	D	0	0	0	0	0	0	0	0
798	D	D	D	D	D	D	D	D	D	0	D	D	0	0	D	D
1127	S	S	D	D	D	0	0	0	S	S	D	D	D	0	D	D
784	D	0	D	D	S	S	0	S	0	0	0	0	S	S	D	D
489	D	D	D	D	S	S	0	S	D	0	S	S	S	S	0	S
Total																
D	7	7	9	9	5	6	5	6	5	2	6	6	5	1	7	6
S	1	1	0	0	3	2	0	2	2	3	1	1	2	3	0	1
0	1	1	0	0	1	1	4	1	2	4	2	2	2	5	2	2
Juvenile females																
1457	D	0	0	0	0	D	D	D	D	D	D	D	S	0	0	0
1491	D	0	D	D	D	0	D	D	D	D	D	D	S	S	S	S
1439	D	D	D	D	S	D	0	0	D	0	D	D	D	S	D	D
1443	D	0	D	D	S	S	D	D	D	S	D	D	D	0	D	D
1461	D	D	D	D	D	0	D	D	S	S	D	D	D	0	D	D
1452	S	S	S	S	D	0	D	D	D	D	D	D	0	D	D	D
1426	S[e]	D	D	D	S	S	0	S	D	D	D	D	D	D	D	D
1482	D	0	D	D	D	0	D	D	D	D	D	D	D	0	D	D
1157	D	D	D	D	D	0	D	D	0	D	D	D	D	0	D	D
1493	D	0	D	D	D	D	0	D	D	D	D	D	0	D	D	D
1431	0	0	0	0	D	0	0	0	D	D	D	D	0	0	0	0
Total																
D	8	4	8	8	7	3	7	8	9	8	11	11	5	3	8	8
S	1	1	1	1	2	2	0	1	1	2	0	0	2	2	1	1
0	1	6	2	2	1	6	4	2	0	1	0	0	3	6	2	2

[a] Side which male was placed: R=right, L=left.

[b] Time spent within 150 cm of either stimulus bird.

[c] Number of feeding bouts at either cage.

[d] Courtship displays within 150 cm of either stimulus bird.

[e] All underlined outcomes were discarded for analysis because of side preferences (see text).

Table VII-3. Outcome of male choice between adult and juvenile female black-billed magpies. A=adult female; J=juvenile female, 0=no choice recorded.

	Female Stimulus Pairs															
Adult: Juvenile:	RW-S (L)[a] SR-- (R)				SY-Y (R) S-RG (L)				S--G (R) S--B (L)				S--G (L) S--B (R)			
Chooser Band Number	T[b]	F[c]	B[d]	All	T	F	B	All	T	F	B	All	T	F	B	All
Adult males																
1260	A	A	0	A	A	0	0	0	A	A	J	0	J	0	0	0
1261	0	A[e]	J	J	J	J	0	J	J	J	J	J	A	A	0	A
1486	A	0	0	0	J	J	0	J	A	J	0	0	0	A	0	0
1481	J	0	0	0	0	0	0	0					A	A	0	A
1495	J	J	A-J	0	A	A	A	A	0	0	A-J	0	A	0	A-J	0
927	J	0	A-J	A	A	A	0	A	0	J	0	0	A	0	0	0
Total																
A	2	1	0	2	3	2	1	2	2	1	0	0	4	2	0	2
J	3	1	1	1	2	1	0	2	1	2	2	1	1	0	0	0
0	1	3	5	3	1	2	5	2	2	1	3	4	1	3	6	4
Juvenile males																
1455	A	A	0	A	A	J	0	0	J	J	J	J	A	0	0	0
1459	J	J	A-J	0	A	0	0	0	A	0	J	0	J	0	0	0
1480	0	J	0	0	A	A	0	A	A	A	0	A	A	A	0	A
1468	J	J	0	J	J	J	J	J					0	0	0	0
1427	J	0	A-J	0	A	J	J	J	A	0	J	J	J	J	0	J
1474	0	0	A	A	A	0	0	0	J	0	0	0	A	A	0	A
----	0	J	A-J	0	A	A	A-J	A	J	A	A	A	A	J	A	A
Total																
A	1	1	1	2	4	1	0	2	1	1	1	2	4	2	1	3
J	1	3	0	1	1	3	2	2	3	1	3	2	0	1	0	1
0	3	2	6	3	0	2	5	3	0	3	2	2	1	3	6	3

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[a] Side which female was placed: R=right, L=left.
[b] Time spent within 150 cm of either stimulus bird.
[c] Number of feeding bouts at either cage.
[d] Courtship displays within 150 cm of either stimulus bird.
[e] All underlined outcomes were discarded for analysis because of side preferences (see text).

Table VII-4. Comparison of different methods of analysis of mate choice in black-billed magpies as applied to the data presented in Chapter III. Numbers of choices are calculated as totals from Tables VII-1 to VII-3; choices: A=adult, J=juvenile, D=dominant, S=subordinate, O=no choice.

Method of Analysis	Female Choice				Female Choice				Male Choice			
	A	J	O	Difference	D	S	O	Difference	A	J	O	Difference
Time spent nearby	44	15	20	$P<0.001^{a}$	51	14	11	$P<0.001^{a}$	21	12	9	$P=0.081^{a}$
Feeding bouts	28	11	32	$P=0.005^{a}$	34	16	30	$P=0.008^{a}$	11	12	9	$P=0.50^{a}$
Courtship display	31	10	38	$P<0.001^{a}$	61	3	16	$P<0.$[illegible]01^{a}	4	8	38	$P=0.19^{a}$
Homogeneity[b]	$X^2=10.18$			$P=0.038$	$X^2=26.42$			$P<0.001$	$X^2=35.8$			$P=<0.001$
All[c]	37	9	21	$P<0.001^{a}$	61	4	11	$P<0.001^{a}$	15	10	21	$P=0.21^{a}$

[a] Binomial one tailed probabilities: based on the ratio of choices A:J and D:S.

[b] Test for homogeneity: probability based on 3x3 contingency table.

[c] All three variables considered, results as presented in Chapter III.

of motivation in magpies may well have affected the intensity of courtship displays, which ranged from very intense to merely approaching one of the two stimulus birds, without displaying. In the latter case no choice would have been recorded for the trial had only courtship displays been used in the analysis. However, if an individual spent more time near one potential partner than another, it may be more likely to mate with the former, despite the many factors that could influence its choice between "spending time with" and "mating with" that individual. This seems to be the reasoning prevailing in the current literature (eg. Bateson 1983). I believe, therefore, that recording the time spent nearby as well as the number of feeding bouts *in addition* to the courtship displays adds valuable information and, in the case of this study, lowered the number of trials in which no choices would have been recorded.

In all probability, the recording of actual matings or pair-formations (as was also done in this study, see Chapter III) yields the most accurate results in the study of mate choice. However, such is not always possible, either because of the behaviour of the animals or because of the nature of the questions being asked. The present comparison of the analysis of different variables suggests that the conclusions drawn either from each one singly or all combined are essentially the same. However, recording several variables seemed intuitively to provide more reliable results.

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VIII. Appendix 3

CLUTCH SIZES OF JUVENILES AND ADULTS IN THE TWO SEXES

Table VIII-1. Clutch size of captive black-billed magpies listed according to age and sex. Each number represents one clutch sired by one male or produced by one female.

	Males		Females	
	adult	juvenile	adult	juvenile
	7	4	7	4
	5	5	5	5
	5	2	7	5
	7	5	7	7
	7	6	6	2
	5	6	7	5
	6	2	7	5
	6	7	8	6
	7	7	6	6
	6	6	3	2
	7	3	8	7
	7	8	4	6
	8	4		7
				6
$\bar{x}$:	6.3	5.0	6.3	5.2
s.d.	±1.0	±1.9	±1.5	±1.6

PARENTAL INVESTMENT EXPERIMENTS DURING THE NESTLING PERIOD

It has been mentioned in Chapter IV that breeding success post hatching was very poor during this study. Most hatchlings died within 5 to 10 days, which was too early to examine parental investment of males during the nestling period. Only a small number of males was caring for young past hatching. This small sample size did not allow comparisons between age groups nor between dominance categories. The performance of these males during the experiments as described in Chapter IV is presented for each male individually in the following tables. An "A" indicates an adult, a "J" a juvenile male. Superscripts indicate the rank in a group of ten males (see Chapter II). Where more than one male was recorded, an average for each age group (indicated by an "A" or "J" without superscript) is presented at the bottom of the tables.

With these preliminary results it is intended to stimulate future studies and to point out some possible trends in male parental behaviour throughout the reproductive cycle. Males of both age groups did not seem to change their effort in feeding in a constant pattern (Tables IX-1 and IX-2). However, there seemed to be an overall increase in the investment in defense against a potential predator by adult males (Tables IX-3 and IX-4). During the territory defense experiments (Tables IX-5 to IX-7) only the average number of contacts seemed to increase steadily (Table IX-6), while the average number of attacks decreased (Table IX-7). It would be premature to draw conclusions from these data. However, these tables suggest that it is possible to monitor changes in parental behaviour of magpies throughout the reproductive cycle and to supplement the results presented in Chapter IV.

Table IX-1. Number of visits at feeders by male black-billed magpies during feeding experiments.

Male	10d[a]	15d	31d	41d
A^1	27	44	11	
A^2	57	47	59	58
A^1	4	81	59	54
A^2	122	113	13	
A^3	10	68	58	68
A^5	36	31	8	
J^4	1	1	0	
J^2	47	79	48	
A	62.7	64.0	34.7	59.7
J	24.0	40.0	24.0	

[a] days after clutch initiation.

Table IX-2. Total time (seconds) spent in searching by male black-billed magpies during feeding experiments.

Male	10d[a]	15d	31d	[illegible]
A1	207	447	96	[illegible]
A2	398	282	397	[illegible]
A1	11	369	478	[illegible]
A2	510	616	57	[illegible]
A3	80	519	550	546
A5	569	445	74	
J4	0	2	0	
J2	124	452	187	
A	295.0	446.3	275.3	414.7
J	62.0	226.0	93.5	

[a] days after clutch initiation

Table IX-3. Total time (minutes) of uttering the harsh note by male black-billed magpies during the exposure to a potential predtor (cat).

Male	17d[a]	33d	42d
A^2	14	15	15
A^3	0	10	13
A^1	15	15	15
A^2	5	10	
A^5	15	15	
A	9.8	13.0	14.3
J^2	4	12	

[a] days after clutch initiation

Table IX-4. Total time (seconds) spent closer than 150 cm of a potential predator (cat) by male black-billed magpies.

Male	17d^a	32d	42d
A^2	639	842	874
A^3	0	0	0
A^1	189	387	380
A^2	0	0	
A^5	244	601	
A	214.4	366	418
J^2	0	0	

^{a}days after clutch initiation

Table IX-5. Time (seconds) spent closer than 150 cm to a "territory intruder" by male black-billed magpies.

Male	18d[a]	33d	43d
A^2	468	198	4
A^3	635	639	1114
A^1	945	1129	1200
A^2	0	40	
A^5	904	685	
A	590.4	538.2	772.7
J^2	1165	901	

[a] days after clutch initiation

Table IX-6. Number of contacts with the cage of the "territory intruder" by male black-billed magpies.

Male	18d[a]	33d	43d
A^2	22	11	0
A^3	2	29	44
A^1	47	54	77
A^2	0	0	
A^5	85	83	
A	31.5	35.4	40.3
J^2	37	52	

[a] days after clutch initiation

Table IX-7. Number of attacks at the "territory intruder" by male black-billed magpies

Male	18d[a]	33d	43d
A^2	26	1	0
A^3	0	13	22
A^1	14	12	11
A^2	0	0	
A^5	27	20	
A	13.4	9.2	6.6
J^2	0	0	

[a] days after clutch initiation

X. Appendix 5

METHODS OF TRAPPING AND SEXING

Trapping magpies with circular funnel traps (Alsager et al. 1972) proved to be very successful with juvenile birds, but only moderately so with adults. It was possible to trap up to 10 juveniles over one evening-morning session, but a total of only three adults was caught in such traps over two seasons combined. A relatively successful, but time-consuming, method for trapping adults was to capture them with nooses (Scharf 1985b). Adults were also successfully trapped using a large funnel trap, which was used for part of the second season. The measurements of the funnel were the same as those described by Alsager et al. (1972), but the cage was one of the pens at the outdoor aviary, measuring 19.2 x 2.1 x 2.1 m. Besides many juveniles, 11 adults were caught in this trap during a period of 4 weeks. The relatively successful use of this large trap may have been due, in part at least, to the presence of captive magpies in adjacent pens which may have functioned as decoys and attracted other birds.

The method of sex determination described by Scharf (1985a) was accurate in 94% of the cases (sex of 97 birds was verified either by dissection or behaviourally during the breeding season). This level of accuracy was similar to the 95% for juveniles and 99% for adults recorded by Scharf (1985a) using this method. It is unfortunate, however, that Scharf (1987) did not publish Table X-2 from his thesis (Scharf 1985a) in this paper, since it is easy to apply and was the basis for sex determination in this study.

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