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THE ROLE OF SOCIAL DOMINANCE IN WINTER FLOCKS OF BLACK-BILLED MAGPIES

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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Date........January 24/93..................

ABSTRACT

The functional role of a dominance hierarchy, as it pertains to the partitioning of food resources, was examined in captive winter flocks of black-billed magpies (*Pica pica*). Conventional wisdom predicts that birds of lowest social status in a dominance hierarchy would have the greatest difficulty gaining access to limited resources. To test this hypothesis, 17 captive flocks (5 birds/flock) of marked magpies in which the dominance relationships were known, were subjected to conditions of food limitation. The proportional amount of weight lost by an individual during the deprivation period was used as a measure of a bird's efficiency in acquiring enough food to balance the demands of activity. Experiments carried out during 1981-82 suggested that birds of intermediate dominance rank were under greater energetic stress during periods of food deprivation than either dominant or subordinate birds. Similar experiments conducted during the winter of 1982-83 showed significant differences in weight loss between birds of different rank: birds ranked 3 and 4 lost more weight than birds ranked 1, 2 and 5. I present a model that incorporates behaviors observed during periods of food limitation and which predicts that (1) birds of low social status are able to gain access to limited food resources because of the behavioural tolerance shown towards them by dominant, high ranking-birds, and (2) birds of intermediate rank have more frequent and/or more intense encounters resulting in lower access to food and higher energetic demands than for birds at either end of the dominance hierarchy.

Additional experiments conducted on captive flocks indicated that birds which differed greatly in dominance rank spent more time feeding together than birds of similar rank. Consequently, the most dominant and most subordinate birds spent significantly more time at the food source than birds of intermediate rank.

Field studies were initiated to determine whether free-ranging flocks of magpies associate in a manner similar to that predicted by aviary studies. Results indicated that a linear peck-dominance hierarchy was established, similar to that described for captive flocks. Associations of individuals, at a spatially limited food source, indicated that a high-ranking (dominant) bird frequented the feeder together with a low-ranking (subordinate) bird more often than predicted by chance. However, it

was also determined that associations among birds of subordinate status were more frequent than predicted by chance, possibly because all birds in the subordinate category were females, and females have shorter individual distances than males. Consequently, females allow other females to approach more closely than do males and thus permit access to food.

If dominance influences survival, one would predict that effective signals of dominance should evolve. Among magpies, body size was positively correlated with dominance status. However, this correlation was a consequence of females being both smaller than and subordinate to males. The relationship between body size and dominance status within each sex indicates that only among males is there a positive relationship, hence large males have priority of access to food over small males. As a result during periods of severe food limitation in winter, large males would be predicted to survive better than small males, producing an increase in sexual size dimorphism among overwintered magpies. A morphometric analysis of juvenile and adult populations of male magpies supports this prediction.

The proposed behavioral model was used to predict payoffs to birds of different dominance status. A simulation based on the behavioral model predicted the net payoffs to birds according to dominance status. These results support the idea that birds intermediate in rank are under greater energetic stress than birds at either end of the dominance hierarchy.

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I. INTRODUCTION

RATIONALE

The evolution of social behavior should occur only if individuals of a given species experience greater fitness within a group than by living alone (Alexander 1974, Wilson 1975, Bertram 1978, Wittenberger 1981). In avian social systems agonistic interactions among conspecifics are often the means by which individuals assess one another's combative abilities (Scott and Fredericson 1951, Gauthreaux 1978, Wittenberger 1981). The criteria used to assess combative abilities are immaterial, however, the outcome of agonistic encounters establishes the dominance status of individuals and hence their relative access to particular resources. Groups of individuals are often arranged in a linear dominance hierarchy, from the most dominant (alpha) bird to the most subordinate (omega). It is this type of social organization that has been suggested as the mechanism promoting a number of population phenomena discussed below.

Dispersal

Gauthreaux (1978) suggests that, when resources are limiting, an increase in competitive interactions among conspecifics will force subordinates away from desired resources. Therefore, the dominance status of such "an individual can be expressed in terms of the distance it has moved from its place of birth or in terms of the quality of the habitat it occupies, or both" (Gauthreaux 1978:27). Among dark-eyed juncos (*Juncus h. hyemalis*) dominant birds apparently exclude subordinates from preferred winter habitats (Ketterson and Nolan 1982, 1983), forcing them to disperse further south in search of suitable habitats. The same reasoning has been used to explain the dispersal of starlings (*Sturnus vulgaris*) (Davis 1959) and wood-pigeons (*Columba palumbus*) (Murton *et. al.* 1966).

Mate Selection

Studies of species that lek on arenas, such as the white-be (*Manacus manacus trinitatis*) (Lill 1974) and sage grouse (*Centroce* (Wiley 1973), show that dominant males, often determined throug competition, copulate more frequently than subordinates. It is fro that dominance has been linked to reproductive success.

Nest Site Selection

Gauthreaux (1978) suggests that subordinate individuals wo from preferred nesting habitat if such areas were in short supply. (1969), and Watson and Moss (1970) suggest that dominant birds sooner than subordinates and therefore have a greater chance of addition, data collected on red-winged blackbirds (*Agelaius phoen* dominant males appear to acquire superior territories, attracting settle on their territories (Searcy 1979).

Survival

It has been suggested that overwinter mortality is greater dominant birds in flocks of silvereyes (*Zosterops lateralis*) (Kikkav juncos (Fretwell 1969), and wood pigeons (Murton *et.al.*: 1966), the lack of access by subordinates to limited food resources. Sin have priority of access to resources, it follows that when resour subordinate birds would be the most likely to do without. Gauthre when food resources are low and high quality habitats are saturat birds, subordinates must disperse or do without.

The important underlying assumptions concerning the func hierarchies are: (1) that dominant animals have priority of access (2) they survive best under conditions of limited food availability probability of survival diminishes as individuals move down the hi 1975, Gauthreaux 1978, Wittenberger 1981). On the other hand, abundant all individuals, regardless of dominance rank, survive (Wilson 1975, Krebs and Davies 1979, Mair and Mair 1970, Gauthreaux 1978, Wittenberger 1981). Although references on dominance behavior pervade the literature, few studies (Kikkawa 1980, Smith *et. al.* 1980, Ketterson and Nolan 1983) have critically examined the functional role played by dominance hierarchies relative to the acquisition of food by individually-marked birds of known social dominance.

The aim of this study was to examine the nature of dominance hierarchies within winter flocks of black-billed magpies (*Pica pica*) and to determine whether they function to partition food relative to dominance status. This study is reported in five parts

1. Deprivation Experiments

In an outdoor aviary I examined the impact of limited availability of food (less than required for daily maintenance) on weight loss among individuals in captive flocks of magpies. I used the proportional amount of weight lost by an individual as a measure of its ability to acquire sufficient food to maintain itself over time, and hence to survive.

2. Aggression

If dominance status is established through agonistic interactions, then asymmetries in the nature of encounters among individuals should provide a measure of the relative energy expended by flock members. Furthermore, asymmetries in the time spent by birds feeding at a limited food source should reflect the amount of food acquired and hence their ability to avoid weight loss.

3. Field Experiments

To examine the generality of the aviary experiments, dominance relationships among marked free-ranging magpies in winter flocks were determined and asymmetries in the frequency of association among flock members, while attempting to gain access to a spatially restricted food source, were noted.

4. Size-Dominance Relationships

If dominance status within magpie flocks influences survival of an individual, one would predict that differences in morphological characteristics may act to signal dominance status (Rohwer 1975). I compared morphometric characters of flock members with their dominance status to test this prediction.

5. Size Dimorphism

If size is related to dominance, and dominance is related to access to food, then, larger birds should survive better than smaller ones. I compared external morphological measurements of juvenile and adult populations of both sexes to test this prediction.

II. DEPRIVATION EXPERIMENTS

Dominance and Its Effect on Weight Loss of Captive Black-billed Magpies (*Pica pica*) During Periods of Food Deprivation: A Behavioral Model

ABSTRACT

Conventional wisdom implies that birds of lowest social status in a dominance hierarchy have the greatest difficulty in gaining access to a limited resource (food). Thus birds, such as black-billed magpies (*Pica pica*), existing under conditions of prolonged food limitation, would be expected to lose weight in relation to their social status (highest, least; lowest, most). To test this hypothesis 17 caged groups of five magpies of known dominance status were subjected to limited food during the winters of 1981-82, and 1982-83. Although evidence for 1981-82 suggested that birds intermediate in rank were most stressed during periods of imposed food deprivation, there were no significant differences in the proportional weight loss among members of the hierarchy. However, similar experiments performed during the winter of 1982-83 showed that there were significant differences in weight lost among ranks; birds ranked 3 and 4 lost more weight than birds ranked 1, 2, and 5. Therefore, it is suggested that birds of intermediate rank are at a greater energetic disadvantage during periods of food limitation than birds at either end of the dominance hierarchy. These results do not support the traditional view of how dominance hierarchies function.

INTRODUCTION

Black-billed magpies (*Pica pica*), like other members of the Corvidae, are gregarious for at least part of the year (Linsdale 1937, O'Halloran 1961, Goodwin 1976, Baeyens 1979). Flocks that form during autumn and winter are predominantly composed of juveniles, with a few second-year and older birds. The organization within these flocks appears to be hierarchical (Baeyens 1981), similar to that described by Lorenz (1931, 1938) for jackdaws (*Corvus monedula*), by Brown (1963) for Steller's jays (*Cyanocitta stelleri*), and by Yom-Tov (1974) for hooded crows (*Corvus corone*).

During winter, in the northern part of the magpie's range, snow cover may remain for long periods of time, potentially restricting food resources. Access by flock members to food resources is vital to their survival. However, because flocks are organized as a dominance hierarchy, one would predict that birds of high status would have priority of access to these limited resources and consequently have a greater chance of survival during periods of food deprivation (Wilson 1975, Gauthreaux 1978, Wittenberger 1981).

In this paper I report on aviary experiments that tested the hypothesis that dominant individuals will lose less weight than subordinates when faced with a limited food resource.

METHODS

Magpies were caught in baited circular-funnel traps (Alsager *et. al.* 1972) during the fall of 1981-82, and 1982-83 in the city of Edmonton, Alberta, Canada. Each bird was weighed on a triple-beam balance, measured with calipers (Appendix 4), individually marked with colored leg bands, and placed in outdoor aviaries. Flight cages measuring 5.8 m x 2.4 m x 2.1 m high were contiguous to an enclosed room measuring 2.1 m x 2.4 m x 2.1 m. Plywood partitions separated the flight cages, visually isolating birds from those in adjacent cages. Each group of birds caught at a given trapping station was housed together in a separate cage. All birds used in both years were juveniles. A period of at least 3 weeks was given to all birds in order to acclimate to the penned conditions. Individuals were then randomly selected to form new groups, seven in 1982 and ten in 1983, of five birds each. To my knowledge, no birds in these new flocks had had previous social contact.

The dominance status of flock members was assessed after they had spent at least 3 weeks together. Dominance was determined by recording from a blind the outcome of agonistic encounters (wins versus losses) between individuals over a food source. A win was scored when one bird either actively displaced another from the food source or caused another to withdraw in a submissive manner (Baeyens 1981). By ranking the birds according to their wins over other flock members, a linear hierarchy among flock mates was determined for nearly all flocks.

When the dominance rank of all birds was known, the food supply (pelleted dog food) was lowered below that needed for daily maintenance at a rate of 2.5% every 2 days in 1981-82 and 1.25% every 2 days in 1982-83. The amount of food needed for daily maintenance was approximated just prior to the period of deprivation by subtracting the amount of food disappearing from the total each day, averaged for the number of birds in the cage. All food, placed in a plastic container from which only two birds could feed at the same time, was located in the center of the aviary.

Each bird was weighed at the start of the deprivation period and at a similar time of day every 4 days thereafter for the duration of the experiments. The deprivation period was terminated when it appeared that the weight lost by birds was adversely affecting their normal flight response. Subsequently, dominance status was assessed in order to determine whether the rank of any bird had changed during the 20 day deprivation period.

Weight loss was used as an index of potential survival. This index is a measure that incorporates a bird's morphological, physiological and behavioral characteristics (Figure II-1).

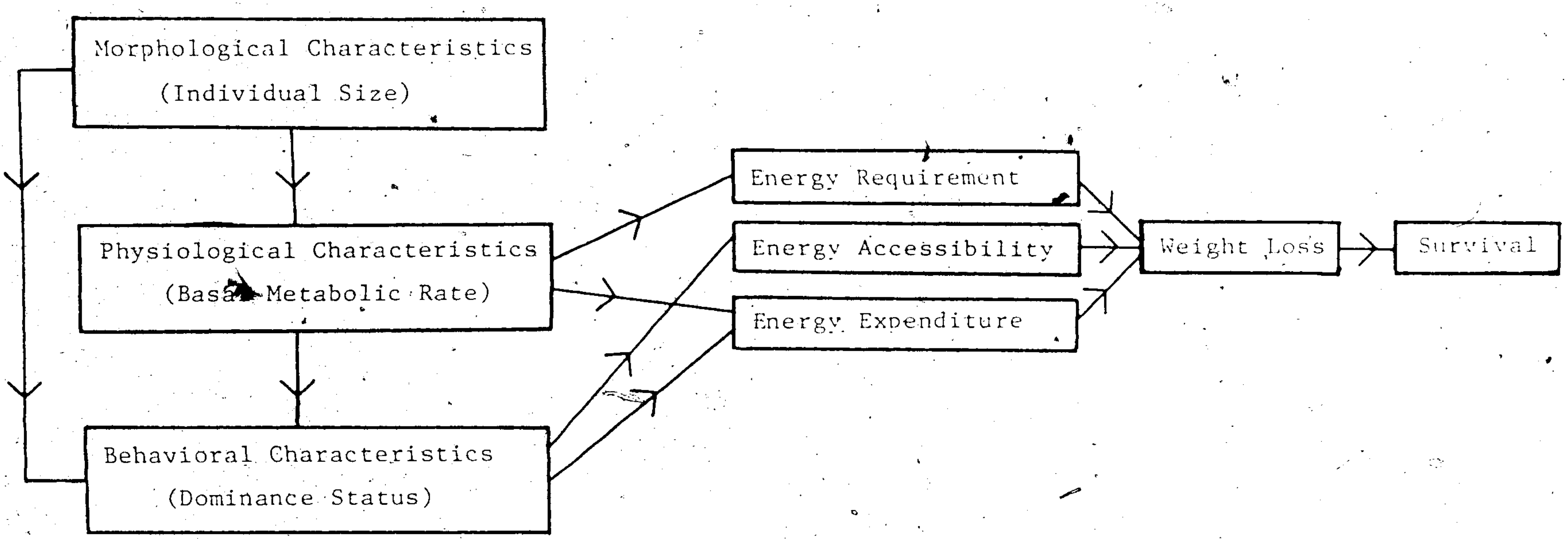

Figure II-1. A bird's morphological, physiological and behavioral characteristics influence directly or indirectly its energy budget, and as a result, determine whether an individual gains, loses, or maintains its body weight during periods of food deprivation, and ultimately whether it survives.

RESULTS

Agonistic encounters between captive individuals ranged from mild threats to violent pecking squabbles. The more violent encounters involved one or both birds pecking at the head, legs, tail, or back of the other. Occasionally one bird chased another around the cage attempting to pull the other's rectrices or kick the other while in flight. This was often accompanied by loud 'harsh' or 'shriek' notes (Baeyens 1979) given frequently by the fleeing bird. Subtle encounters between birds resembled aggressive encounters but lacked their intensity. Submissive birds often exhibited 'chin-up,' 'wing-flickering,' or 'horizontal wing quivering' displays (Baeyens 1979) when either approaching or being approached by more dominant birds.

Hierarchies of the 17 caged flocks were nearly all linear, however, because of small flock size this linearity could not be verified statistically according to the methods of Appleby (1983). In all cases hierarchical relationships subsequent to the deprivation experiments remained the same as those assessed prior to experimentation .

Of the 85 magpies involved in the winter deprivation experiments of 1981-82 and 1982-83, none gained more than 2% of its original weight, nine fluctuated by less than 2%, and 76 lost more than 2% of their original weight (Tables II-1, and II-2). Despite the pattern which suggested that birds ranked 3 and 4 lost more weight than birds ranked 1, 2, and 5, in 1981-82 there was no significant difference in weight loss among birds in that year (Table II-1). The amount of weight lost by magpies of different ranks in the remaining captive flocks (1982-83), disregarding sex composition, was significantly different (Table II-2). The non-parametric equivalent of the Student-Newman-Keuls Multiple Comparison Test (Zar 1974) showed that Rank 2 lost significantly less weight than any other rank, however, birds of Rank 3 and 4, although not different from one another, lost significantly more weight than birds of Rank 1 and 5 which were also not different from one another (Rank 2 < Rank 1 $\leq$ Rank 5 < Rank 3 $\leq$ Rank 4). In addition a non-parametric Friedman's test (randomized block design) was done using only the ranked weight loss within each cage. This enabled me to combine the results of both experiments (Table II-1, II-2). These results showed a significant difference in weight loss among ranks (Freidman's Test, X^2=

Table II-1. Total percentage weight change (final/initial weight x 100) of caged magpies over a period of food deprivation during the winter (Jan. 13-29) of 1981-1982. Most dominant=1, most subordinate=5.

Cage	Dominance Rank				
	1	2	3	4	5
1	-6.2 (214.2-M)[a]	+1.7 (183.5-F)	-1.8 (201.0-F)	-13.3 (201.0-F)	-29.7 (185.3-F)[c]
2	-6.8 (213.5-M)	-2.1 (236.5-M)	-10.1 (191.4-F)[b]	-18.7 (184.8-F)[b]	-6.3 (174.0-F)
3	-7.3 (233.7-M)	-8.0 (210.2-M)	-8.3 (204.2-M)	-20.8 (229.3-M)	-7.6 (205.7-M)
4	-6.1 (225.3-M)	-9.7 (210.7-M)	-13.0 (195.9-F)	-17.4 (208.4-F)	-6.8 (223.9-M)
5	-1.2 (200.3-M)	-18.3 (207.1-M)	-2.8 (206.6-M)	-5.0 (174.8-F)[c]	-0.6 (173.9-F)
6	-8.0 (195.7-M)	-9.5 (175.8-F)	-4.0 (169.4-F)	-11.6 (174.9-F)	-12.2 (177.7-M)
7	-13.1 (225.7-M)	-3.3 (217.6-M)	-12.5 (169.4-F)[c]	-4.2 (168.6-F)	-8.0 (179.7-M)
Mean[d]	-6.9	-7.0	-6.0(-7.5)	-13.5(-13.0)	-6.9(-10.2)
Rank[e]	2.4	2.4	3.1	4.1	2.9

[a] Original weight (gms) and sex of the bird in parentheses: M=male, F=female.

[b] Died before experiment terminated; weight loss based on weight on the day of death.

[c] Died and partially cannabilized before final weighing; weight at termination of experiment estimated.

[d] Mean for birds that survived to the end of the experiment. Values in parentheses includes birds that died before the termination of the experiment as well as those for which final weight had to be estimated.

[e] Mean rank based on the rank assigned to the weight loss of individuals within a given cage.

Table II-2. Total percentage weight change (final/initial weight x 100) of caged magpies over a period of food deprivation during the winter (Jan.13-Feb.6, 1982-1983). Most dominant=1, most subordinate=5.

	Dominance Rank				
Cage	1	2	3	4	5
8	-8.2 (229.6-M)[a]	-3.8 (184.5-F)	-13.2 (183.7-F)	-10.8 (209.3-M)	-9.2 (173.4-F)
9	-5.5 (200.3-M)	-4.5 (205.3-F)	-4.7 (175.6-M)	-6.4 (179.1-F)	-7.8 (175.6-F)
10	-9.1 (208.2-F)	-0.4 (205.3-M)	-3.3 (206.4-M)	-24.4 (193.4-F)	-4.6 (202.1-F)
11	-5.9 (224.6-M)	-5.2 (219.3-M)	-9.6 (183.1-F)	-10.3 (210.7-F)	-6.3 (167.4-F)
12	-5.1 (229.7-M)	-0.6 (176.1-F)	-11.7 (188.0-F)	-6.9 (184.3-F)	-4.4 (179.3-F)
13	-6.9 (211.6-M)	-6.6 (204.3-M)	-15.7 (208.3-M)	-9.1 (202.5-F)	-15.6 (200.7-F)
14	-7.9 (201.3-M)	-8.0 (230.7-M)	-6.4 (217.3-M)	-8.2 (210.0-F)	-4.3 (183.4-F)
15	-1.2 (213.4-M)	-0.1 (181.3-M)	-1.0 (209.3-M)	-5.4 (180.7-M)	-19.4 (179.0-M)[c]
16	-7.2 (225.4-M)	-3.6 (221.2-M)	-5.0 (218.9-M)	-17.8 (167.4-M)	-32.6 (167.7-F)[c]
17	-6.8 (192.4-F)	-6.6 (181.6-F)	-6.9 (182.6-F)	-4.9 (172.1-F)	-24.1 (166.6-F)[c]
Mean[d]	-6.2	-3.7	-7.9	-10.7	-7.5 (-12.8)
Rank[e]	2.6	1.4	3.9	4.3	2.9

[a] Original weight (gms) and sex of the bird in parentheses: M=male, F=female.

[b] Died before experiment terminated; weight loss based on weight on the day of death.

[c] Died and partially cannabilized before final weighing; weight at termination of experiment estimated.

[d] Mean for birds that survived to the end of the experiment. Values in parentheses includes birds that died before the termination of the experiment as well as those for which final weight had to be estimated.

[e] Mean ranks based on the rank assigned to the weight loss of individuals within a given cage. Cages 15, 16, and 17 not included because birds of Rank 5 were injured before the experiment began.

16.46, $P=0.003$). A multiple comparison test (Sheffe-type confidence intervals, Marascuilo and McSweeney 1977) indicated that Rank 2 lost significantly less weight than Rank 4. Moreover, the pattern of weight loss among ranks indicated that birds of Ranks 3 and 4 are lost more weight than the other Ranks (Rank 2 $\leq$ Rank 1 $\leq$ Rank 5 $\leq$ Rank 3 < Rank 4).

That females are subordinate to males might suggest that females lose more weight than males, however, this was not true in either year (Wilcoxon two-sample test: 1981-82, U=132.5, $P=0.29$ 1982-1983, U=194.5, $P=0.13$). It is noteworthy that of those birds that died in both years, two were of Rank 3, two of Rank 4, and 4 of Rank 5. Birds of rank 3 apparently died of starvation as did one bird of rank 4 (the other died of unknown causes). All but one bird of Rank 5 that died had sustained injuries in pens before the determination of the dominance and were observed to be handicapped during encounters. It is not known whether these birds ranked omega (rank 5) because they were injured or whether they were injured because they were the omega birds. For cages containing injured birds (Table II-2, cages 15, 16, 17), the proportional amount of weight lost according to rank was significantly different (Kruskal-Wallis, H=11.95, $P=0.02$). A multiple comparison test (Marascuilo and McSweeney 1977) indicated that Rank 5 lost significantly more weight than all other Ranks (Rank 2 $\leq$ Rank 3 $\leq$ Rank 1 $\leq$ Rank 4 < Rank 5).

The influence of sex composition within a given flock was examined in order to determine whether it influenced weight loss. This was done by considering only flocks composed of birds of the same sex ratio (2-males, 3-females; 3-males, 2-females; 1-male, 4-females). Regardless of sex ratio within flocks, the pattern of weight loss was similar among ranks increasing in the following order: Rank 2 $\leq$ Rank 1 $\leq$ Rank 5 $\leq$ Rank 3 $\leq$ Rank 4. In addition an examination of the concordance of the ranking of weight loss among all cages, regardless of sex ratio, suggested that the pattern of weight loss was similar (Friedman's Test, X^2= 8.73, P= 0.07).

DISCUSSION

The results obtained in this study show that flocks of captive magpies exhibit linear dominance hierarchies similar to those described by Baeyens (1981), and Trost (per. comm.) for free-living birds. They are characteristic of peck-dominance hierarchies initially described by Schjeldrup-Ebbe (1922) for domestic fowl (*Gallus domesticus*)..

The predicted relationship between weight loss and social rank was not realized; lowest ranked birds did not lose proportionally the most weight. Nor did top-ranked individuals lose the least weight. In fact they lost more weight than birds of Rank 2 in 1982-83. Uninjured omega birds lost less weight than birds of Rank 3 and 4. From this I conclude that birds of intermediate dominance status are the most likely to be at a disadvantage during periods of food deprivation. In addition my results indicate that injured birds lose significantly more weight than uninjured birds. Observations revealed that injured birds bore the brunt of aggressive activities from other members of the flock when food was limiting.

An important question that arises is whether relative weight loss of an individual is indicative of its physiological condition and consequently its potential ability to survive. Murton *et al.* (1971), after examining survival of wood-pigeons (*Columba columbus*), suggested that weight loss and subsequent disappearance were indicative of death. Birds that lost the most weight among flocks were often those that subsequently disappeared. Baker and Fox (1978) determined that when dark-eyed juncos lost weight down to 17 grams, they were dangerously near death and were hence classified as non-survivors. During the course of this study eight individuals died as a result of food deprivation. These individuals lost on average more weight between weighing periods than the average lost by all other birds within their respective flocks (Table II-3). This indicates that birds which died lost weight at a greater rate than birds which survived. To visualize the decline in weight during the course of the experiments I plotted the percentage weight lost by survivors and non-survivors (Fig. II-2). It appears that individuals that lose nearly 10% of their total body weight were unlikely to survive. Recent work by Tatner (pers. comm.) determined that the fat content of magpies (*Pica pica pica*) is approximately 9.2% of

Table II-3. Comparison of the number of times that magpies fell into one of two weight loss categories at each weighing period and that subsequently either survived or died.

Weight Loss[a]	Number	
	Survived	Died
Above Average	51	4
Below Average	28	15
Difference[b]	$P < 0.01$	

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[a] The weight loss of birds which fell on the average value were not included in the analysis (3 cases)

[b] Based on 2x2 contingency table, $X^2 = 11.17$

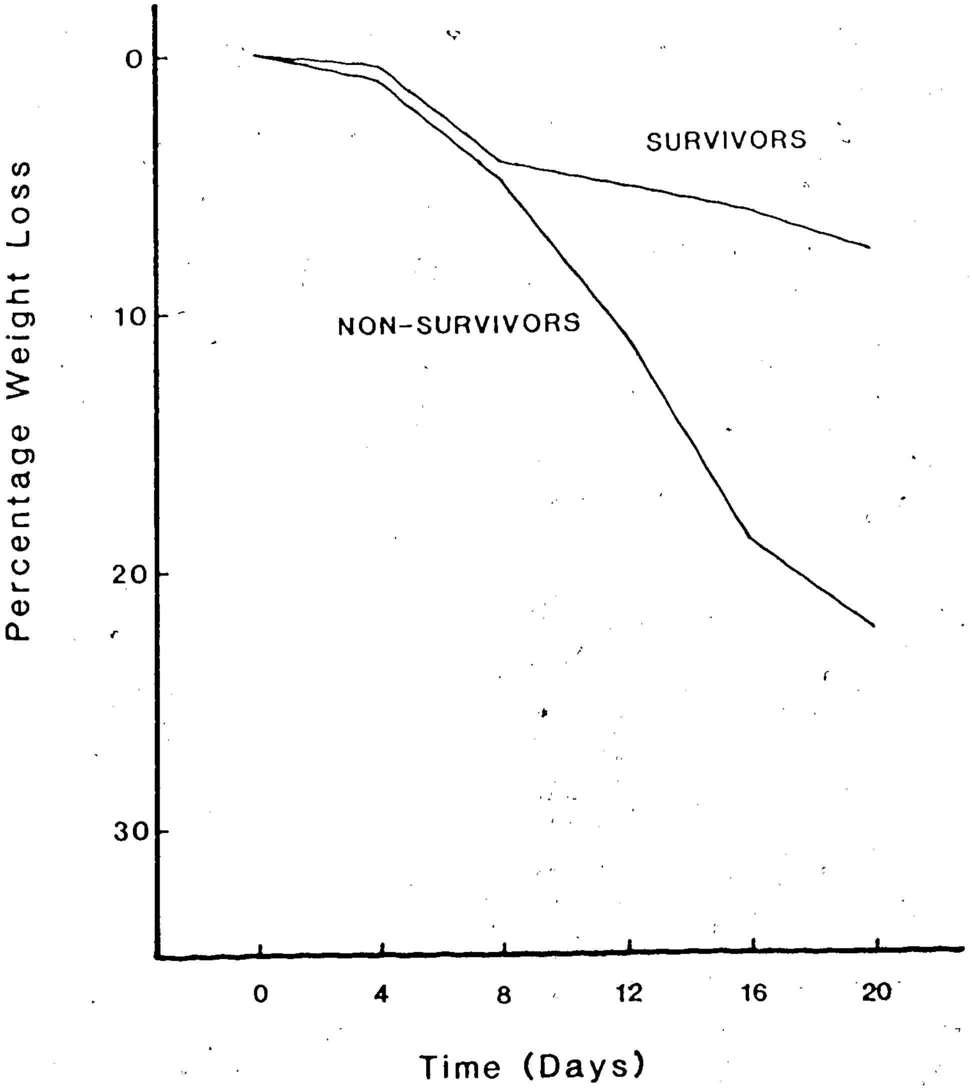

Figure II-2. Comparison of the cumulative percentage weight lost by magpies that survived and died during the 20-day deprivation experiments. Data from 1981-1982 and 1982-1983 have been combined.

its total body weight. Birds that lost 10% of their body weight in this study showed no fat adjacent to their furcula and showed signs of muscle degeneration. I suggest that when birds have lost 10% of their total body weight, they have used up their fat reserves, and must begin to catabolize muscle tissue. I conclude that weight loss in black-billed magpies in this study can be used as a measure of condition, and that when weight loss exceeds 10% of the total body weight, survival of magpies is in jeopardy.

Another important aspect of dominance is the possibility that birds may be interacting with one another differently depending on sex. The preference shown by pairs of birds to associate with one another may reflect differences in behavior between male-male, male-female and female-female encounters. For example, in three of the 17 flocks maintained after the termination of the food deprivation experiments, the alpha and omega birds formed a pair-bond, exhibiting normal pair courtship behavior (Baeyens 1979). In one cage a mated pair went as far as building a nest, incubated eggs and hatched young. This observation has since been confirmed by S.G. Reebs (pers. comm) who is also examining dominance relationships within captive magpie flocks. Although the sex of flock members may influence the intensity, or the type of encounters among individuals, it apparently does not influence the pattern of weight loss resulting from dominance rank. In one flock containing birds of the same sex, the pattern of weight loss was similar to that observed in flocks of mixed sex. Furthermore there was no significant difference between the total proportional weight lost by males and females, although females did experience a greater variation in weight loss in both years (1981: females;mean= 9.8, s.d.=7.5, versus males;mean=7.0 s.d.=4.9; 1982: females;mean= 8.7, s.d.= 5.3 versus males;mean=6.3, s.d.=3.9). This greater variation in weight loss by females suggests that more of them will lose 10% of their weight during periods of deprivation and hence have a greater chance of succumbing. This being so one would predict that after periods of deprivation the sex-ratio could be skewed in favor of males.

Observations of a marked free-ranging population of magpies over a 3-year period indicated a 2:1 sex-ratio in favor of males (Baeyens 1981). Further observations by Trost (pers. comm.) and Scharf (unpublished data) indicates that fewer females than males exist within non-breeding summer flocks. Furthermore, in Edmonton, magpies do not normally breed in their first year, however, of those individuals that were recorded breeding in their first year, all were females. This would tend to decrease the number of females present in the non-breeding population and thereby produce a male biased sex-ratio in these flocks.

Observations of behavior made during the deprivation experiments suggest that birds of intermediate rank experienced greater difficulty in acquiring food than either dominant or subordinate birds. Birds that differed greatly in dominance rank tolerated the close presence of one another; thus dominant birds allowed subordinate birds to feed while excluding birds of closer (intermediate) rank from the food. This behavior is incorporated in a model (Figure. II-3). Differences in the intensity as well as the frequency of interactions may influence an individual's overall energy expenditure. In effect birds of similar rank are denied access to food because of their social rank as well as having the additional energetic demands resulting from more frequent and more intense encounters with birds of similar rank. I therefore propose that these differences in behavioral patterns among members of a dominance hierarchy may modify the energy expenditure (costs) of individuals thereby influencing survival. Addtionally, support comes from a similar sequence of behaviors described by Ketterson and Nolan (1983) for juncos and Rohwer and Ewald (1981) for Harris sparrows (*Zonotrichia querula*). However they suggest that intermediate-ranked birds would be more likely to disperse or migrate greater distances if conditions were unfavorable. In the case of magpies, intermediate-ranked birds may disperse. This could result in dispersers succumbing if they were unable to establish themselves in a more favorable rank position in a subsequent hierarchy. Moreover, if the rank achieved by an individual is a function of the number of other high or low ranking individuals within its flock, then the predictive value of dominance hierarchies as a functional mechanism for characterizing dispersal, migration, or survival is likely to be more complex than originally believed.

I suggest that the effect of the level of agonism and tolerance to approach between birds of different rank can influence patterns of weight loss observed in these experiments. If field observations support the results of the aviary experiments I

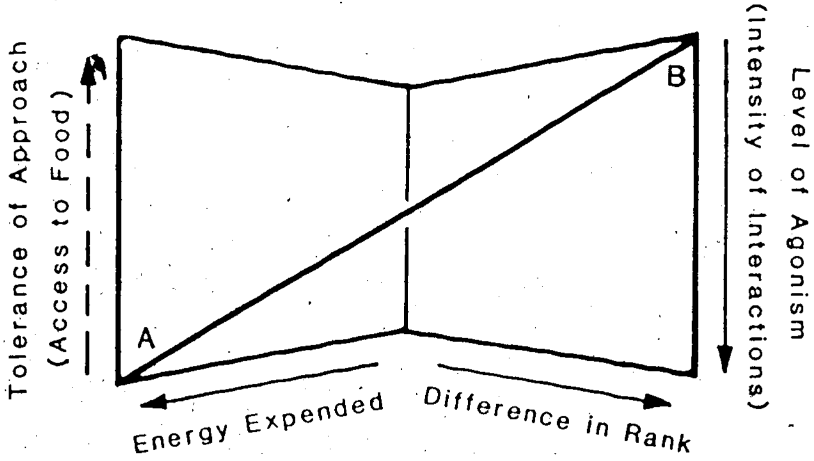

Figure II-3. A model, based on behavior of magpies observed during periods of food deprivation, shows the effect of interaction of rank status, and levels of agonism and tolerance to approach on the energy budget of magpies. Position A: small difference in rank, low tolerance, high levels of agonism resulting in high energy expended. Position B: a large difference in rank, high tolerance, low levels of agonism resulting in low energy expended.

would predict that birds of intermediate rank would be more likely to be eliminated from the population during periodic winter food shortages than higher or lower ranks. If dominance is correlated with size, this would effectively increase overwinter sexual size dimorphism in mapgies. These predictions are considered in subsequent chapters.

III. AGONISTIC INTERACTIONS

Agonistic Interactions Among Captive Black-billed Magpies of Different Dominance Status

ABSTRACT

The types of agonistic interactions occurring between black-billed magpies (*Pica pica*) in captive flocks showing a linear hierarchy were investigated. Rarely did more than two magpies feed together at a single food source that was limited in quantity and accessability. The time spent feeding together by flock members that differed greatly in dominance rank was greater than by birds that were similar in rank. Hence, the most dominant and subordinate birds spent more time together at the food source than did any other combinations of birds in the flock. In addition, the proportion of aggressive to submissive encounters among the members of a flock was greater when the flock was composed of dominant individuals than when composed of subordinate birds. This reflected a higher proportion of aggressive encounters between males than between either females or dyads of mixed sex. These data suggest that the intensity of interaction between birds is influenced not only by dominance rank but also by the sex of the individuals.

8

INTRODUCTION

An examination of captive flocks of black-billed magpies (*Pica pica*) suggests that birds of intermediate rank in dominance hierarchies are subject to the greatest energetic stress as measured by weight loss during periods of food deprivation (Chapter II). A model based on a qualitative assessment of behavior observed during the period of food deprivation predicts that (1) birds of low social status are able to gain access to limited food resources because of the tolerance to the close approach shown towards them by dominant individuals, and (2) birds of intermediate rank have more frequent or more intense encounters which result in higher energetic demands than birds at either end of the dominance hierarchy. The aim of this study was to quantify the nature of the interactions and thereby test the above predictions.

METHODS

Magpies were live-trapped in baited circular-funnel traps (Alsager *et. al*. 1972) during the fall of 1982-83 in the city of Edmonton, Alberta, Canada. The sex of each bird was determined from external measurements (Appendix 2). All birds were individually color-marked with plastic leg bands and placed in separate outdoor aviaries. Flight cages of the aviaries measured 5.8m x 2.4m x 2.1m high and were attached at one end to a room measuring 2.1m x 2.4m x 2.1m. Plywood partitions separated the cages, preventing birds in one cage from seeing those in adjacent cages. Each group of birds caught at a given trapping station was placed in a separate cage. A period of 3 weeks was given for all birds to acclimate to the penned conditions. Birds, which to my knowledge had never been previously associated, were then randomly chosen from each cage to comprise five groups of five birds.

The dominance status of flock members was assessed by recording, from a blind, the outcome of agonistic encounters (wins versus losses) between birds at a centralized food source. A win was scored when one bird either displaced another from the food or caused it to behave in a submissive manner (Baeyens 1979). The results enabled me to arrange all flock members into a dominance hierarchy and thereby assign a rank to each bird. After the dominance relationships were known, flocks were subjected to a diet in which the amount of food (pelleted dog food), was slowly reduced; the amount given was below that needed for daily maintenance of all birds in the caged flocks. In three of these cages the time spent by birds feeding together, during the first 15 minutes after food was introduced, was recorded.

As soon after the deprivation experiments were over all captive flocks were placed on an *ad-libitum* diet for 3 weeks, during which the birds regained the weight they had lost. Subsequently, birds of a given rank were removed from five caged flocks and placed together with other birds of the same rank. All newly formed flocks were then allowed 3 weeks to establish new hierarchies which were determined by the same methods used previously. During observation of the flocks, encounters were recorded as either aggressive or submissive. An aggressive encounter was scored when it ended in actual physical contact and a submissive encounter was recorded when one bird avoided contact either by exhibiting submissive displays or postures or withdrawing from the encounter. Typical aggressive and submissive displays are described by Baeyens (1979).

RESULTS

The amount of time spent feeding together by two individuals of different rank status in each of three captive flocks are given in Table III-1. A significant polynomial regression was found when the percentage of time a dyad spent together was plotted against their difference in rank (Figure III-1). A difference was also noted among birds of different ranks in the total time spent at a food source (Table III-2). Birds ranked 3 and 4 spent much less time feeding than birds ranked 5, 1 and 2. The amount of time spent feeding followed the same order in all three cages: Rank 5>Rank 1>Rank 2>Rank 4>Rank 3.

The magpies of similar ranks, (eg. all alpha birds from five flocks) were reranked in the new flocks. The new hierarchies formed were typical peck-right hierarchies (Table III-3). The proportion of aggressive to submissive encounters among

Table III-1. Time (minutes and seconds) spent by two magpies of different rank feeding together at a restricted food source.

		Hierarchy[a]				
Cage		1	2	3	4	5
8		BW(M)[b]	Y(F)	GR(F)	RB(M)	BR(F)
	BW		0:10	0:57	1:47	14:11
	Y			0:05	0:15	5:55
	GR				0:10	0:10
	RB					0:00
10		BS(F)	RR(M)	GY(M)	GR(M)	S(F)
	BS		0:00	0:00	1:15	14:07
	RR			0:00	3:41	5:09
	GY				0:00	0:35
	RG					0:00
12		WG(M)	YG(F)	BR(F)	SO(F)	S(F)
	WG		0:30	0:05	0:10	12:52
	YG			0:00	0:15	2:46
	BR				0:00	0:00
	SO					0:00

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[a] Hierarchial relationship: 1=alpha, 5=omega.

[b] Sex of bird in parentheses: M=male, F=female.

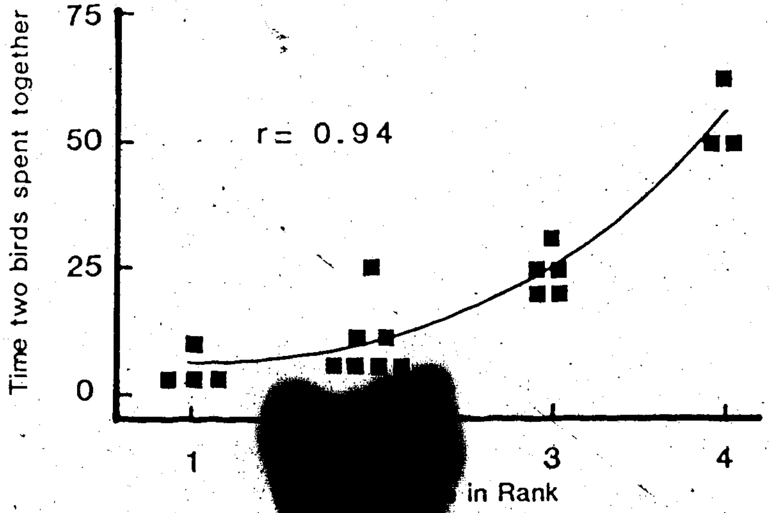

Figure III-1. The relationship between the time spent by two magpies feeding together at a single food source and their difference in rank. Time is expressed as the percentage of total time observed that birds were seen feeding together. An outlier within a Difference in Rank of 3 has been removed. In the graph these percentages have been subjected to an arcsine transformation (equation for the line, y= 18.5-19.0x + y= 18.5 - 19.0 x + 6.89 x^2).

Table III-2. Amount of time (bird-minutes) spent feeding at a single food source by magpies of a given rank.

		Cage 1	Cage 2	Cage 3
Dominance[a] Rank	1	17.08	13.61	15.37
	2	6.42	3.52	8.83
	3	1.37	0.08	0.58
	4	2.20	0.42	4.93
	5	20.27	15.62	19.85
Total		47.33	33.22	49.57

[a] Hierarchial relationship: 1=alpha, 5=omega.

Table III-3. The number of aggressive and submissive (in parentheses) interactions won by captive magpies in flocks of five birds each.

Cage	Previous Rank		Hierarchy[a]					Percent Aggressive
			1	2	3	4	5	
1	1		OR(M)[b]	WB(M)	BW(M)	RY(M)	BS(F)	64.9%
		OR		4(1)	8(2)	0(1)	3(3)	37(57)
		WB			7(2)	2(1)	--	
		BW				5(5)	2(1)	
		RY					6(4)	
2	2		S(M)	BY(M)	RR(M)	Y(F)	YG(F)	65.5%
		S		10(5)	12(2)	12(3)	10(3)	57(87)
		BY			5(4)	1(3)	3(3)	
		RR				1(3)	2(3)	
		Y					1(1)	
3	3		BR(F)	GR(F)	WO(M)	OS(F)	GY(M)	28.4%
		BR		2(7)	1(5)	2(6)	3(3)	21(74)
		GR			4(8)	4(7)	0(5)	
		WO				3(8)	0(3)	
		OS					2(1)	
4	4		G(M)	SO(F)	RB(M)	S(F)	RG(F)	24.0%
		G		3(6)	2(10)	0(7)	1(7)	18(75)
		SO			2(5)	0(5)	2(6)	
		RB				5(2)	3(5)	
		S					0(4)	

continued

Table III-3 (continued)

Cage	Previous Rank		Hierarchy[a] 1	2	3	4	5	Percent Aggressive
5	5		S(F)	BR(F)	WB(F)	OS(F)	WR(F)	0%
		S		0(3)	0(6)	0(5)	0(4)	0(29)
		BR			0(3)	0(2)	0(1)	
		WB				0(2)	0(2)	
		OS					0(1)	

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[a] Hierarchial relationship: 1=alpha, 5=omega.

[b] Sex in parentheses: M=male, F=female.

birds in these five groups differed significantly (Table III-3). Pairwise comparisons (Scheffe-type confidence interval, Marascuilo and McSweeny 1977) revealed that the proportions of encounters among members of flocks composed of birds previously Rank 1 and Rank 2, were significantly more aggressive than among members of flocks composed of birds previously ranked 3 and 4, which in turn, were significantly more aggressive than encounters among magpies of Rank 5. These changes in levels of aggressivity of birds among cages were not found between Ranks within a cage. There was no difference among individuals within a cage in terms of the proportion of aggressive to submissive encounters (Table III-4).

A question arising from these observations is whether sex influences the type of agonistic encounter occurring between interacting birds? A comparison of the nature of the encounters between magpies of the same and opposite sex showed a highly significant difference in the proportion of aggressive and submissive behaviors (Table III-5). Male-male interactions are characterized by a greater proportion of aggressive than submissive interactions ,whereas male-female interactions show nearly equal proportions, and female-female interactions are characterized by greater proportion of submissive behaviors (Male-Male>Male-Female>Female-Female; Table III-5).

DISCUSSION

The results of this study indicate that the greater the difference in dominance rank between individuals, the more time they spend feeding together (Figure III-1). Because of this, birds of intermediate ranks must spend less time feeding than either the alpha (most dominant) or omega (most subordinate) birds. As a result, if food were limiting in quantity and exhausted before all birds gained access to it, certain individuals would lose weight and ultimately succumb. Marler (1955-57) noted that dominant chaffinches (*Fringilla coelebs*) allowed subordinate birds a closer approach than birds of intermediate rank. Similar findings have been reported by Ketterson (1979) and Rohwer and Ewald (1981) for juncos (*Junco h. hyemalis*). Thus it appears that birds of low social status are able to gain access to limited food resources

Table III-4. Number of aggressive and submissive interactions recorded for each bird in every cage.

	Rank						
	1	2	3	4	5	$\underline{P}^a$	Total
Cage 1							
aggressive	15	13	22	13	11		74
submissive	7	4	10	11	8	0.59	40
Cage 2							
aggressive	44	19	20	15	16		114
submissive	13	15	12	10	10	0.24	60
Cage 3							
aggressive	8	10	8	11	5		42
submissive	21	27	24	22	12	0.96	106
Cage 4							
aggressive	6	7	12	5	6		36
submissive	30	22	23	19	22	0.50	116
Cage 5							
aggressive	0	0	0	0	0		0
submissive	18	9	13	10	8		58
$\underline{P}^a$							< 0.01

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[a] Based on 2x5 contingency table

Table III-5. - The number of aggressive and submissive interactions recorded when the interactions were between two males, a male and a female, and two females magpies.

	Male-Male		Male-Female		Female-Female		P[a]
	n	%	n	%	n	%	
Aggressive	53	67.1	68	44.4	12	13.2	<0.01
Submissive	26	32.9	85	55.6	79	86.8	

[a] Based on a 2x3 contingency table ($X^2 = 52.01$)

because of the tolerance shown to their close approach by dominant individuals. These data support the first prediction of the behavioral model, namely that birds of subordinate status will be allowed access to food by dominant birds.

Since no significant difference was evident in the level of aggressiveness among flock members, there is no support for the second prediction of the behavioral model, namely that intermediate ranked birds will have encounters of greater intensity. Therefore different levels of aggression among individuals in different cages can be attributed to all members of a given flock, and from the observations in this study seemed to be related to the dominance status of interacting birds as well as their sex.

The proportion of aggressive to submissive interactions showed significant differences for males and females. The greatest proportion of aggressive interactions occurred in male-male dyads, the least in female-female, and an intermediate proportions in male-female dyads. Marler (1955-57) found similar relationships among chaffinches as did Craig *et. al.* (1982) for Mexican jays (*Aphelocoma ultramarina*). Birkhead (1979, 1982) and Baeyens (1979) noted that the sex of a caged magpie placed on a magpie territory influenced the types of response given by the territorial owner. Males were noted to be more aggressive towards males than females. Baeyens (1979) observed that when presenting territorial magpies with a live decoy, mates would join in aggressive behavior. However as soon as one mate left, aggression would sometimes stop and the remaining bird, if of the opposite sex, would start courting the intruder. Males showed this behavior more often than females, alternating between attacking the decoy in the presence of his mate and courting it in her absence. Birkhead (1979) noted that male magpies tolerate female intruders more than other males, occasionally courting the females. Furthermore, Buitron (1983) has suggested that mate-guarding behavior by male magpies has evolved to eliminate possible extra-pair copulations by intruding males. Lorenz (1938) observed that among jackdaws (*Corvus corone*) only the most subordinate birds (females) formed pair-bonds with the most dominants (males) as Craig *et.al.* (1982) observed for Mexican jays. They also observed that when a dominant male gained access to food, he often allowed the subordinate mate (female) access while keeping other birds, higher in rank than his mate, away from the food. Hence, during periods of extreme food limitation a dominant bird may enhance the survival of its mate or prospective mate by allowing it access to food.

These data suggest that magpies modify the nature of their interactions with other individuals depending on sex and dominance status of the individuals involved.

IV. FIELD EXPERIMENTS

Associations of Feeding Individuals
Relative to Their Dominance Rank
Among Flock Members of Free-ranging Black-billed Magpies

ABSTRACT

A linear peck-dominance hierarchy was recorded in a flock of 15 free-ranging black-billed magpies (*Pica pica*) in Edmonton, Alberta. Birds that differed greatly in dominance rank associated at a food source (fed within 10 cm of one another) more frequently than birds that were similar in rank, enabling subordinates to acquire food in the presence of dominant individuals. The frequency of associations reveal that male dyads associate less than expected, female dyads more than expected, and male-female dyads similar to the frequency predicted by chance. These results support the contention that the sex of interacting birds can influence the nature of the encounters.

INTRODUCTION

Hediger (1941) coined the term "individual distance" when he observed that most animals require a certain distance between themselves and other conspecifics. Burckhardt (1944), Conder (1949) and Hinde (1954) further advanced the idea that individual distance is a fixed area around an individual which is kept free of all others, accomplished either by attacking, threatening or moving away from an intruder. However, Marler's (1955-57) aviary experiments on chaffinches (*Fringilla coelebs*) strongly suggest that individual distance between birds varies according to sex, with female birds associating more closely than males.

Aviary experiments revealed that male black-billed magpies (*Pica pica*) act more aggressively towards other males than females (Chapter III). Further, dominant males often tolerated or associated more closely with subordinates, often females, than with birds that were more similar in rank. In another set of experiments birds of intermediate rank were found to lose more weight than either the dominant or subordinate birds during periods of food deprivation (Chapter II). These experiments suggested that tolerance shown towards the omega bird by the alpha allowed the former access to limited food resources.

It was the aim of this research to determine whether free-ranging magpies, of known dominance rank, associated at a food source in a manner similar to that predicted by the aviary studies. Specifically, do dominant and subordinate birds feed together more frequently at a limited food source than dominant-intermediate, intermediate-intermediate, or intermediate-subordinate dyads?

METHODS

The study area selected was the University of Alberta farm, within the City of Edmonton, where a large population of individually color-marked magpies existed. Birds that were unbanded were captured during the fall of 1982 using baited circular funnel traps (Alsager *et. al.* 1972) or slip nooses (Appendix 3). These birds were then individually color marked and released. Age was determined by plumage characteristics, [illegible] morphometric measurements (Appendix

2).

Platform feeding stations, to which magpies were attracted, were established and maintained at the University Farm during the fall and winter of 1982-83. Agonistic interactions among marked birds attending the feeding station were recorded. Encounters were scored as wins when one bird interacting with a second caused the latter to flee or act submissively. By ranking the birds according to their wins over other flock members, a social dominance hierarchy among flock members was determined. After the ranks of all birds were determined a feeding trough (50 cm long, 10 cm wide, 5 cm high, covered by wire mesh), provisioned with fat and meat, was placed at the feeding station. While birds visited the feeding trough their individual color combinations and their position relative to the metric calibration on the side of the trough were recorded. Birds feeding within 10 cm of one another (determined to be the minimum distance at which agonistic encounters occur) were classified as a feeding association.

RESULTS AND DISCUSSION

By mid-November 1982 a flock consisting of 15 birds was established in the vicinity of the feeding station. Although other birds were occasionally present, individuals that were seen less than 20% of the time were considered transients. In most cases transient birds were seen only once or twice; in all but two cases transient individuals were unmarked. Because all magpies within the vicinity of the feeding station had been individually marked, transient birds had to have travelled at least 1 km in order to be recorded at the site of the feeding station. All birds in the 15 member flock were of local origin. It is possible that the early associations of young birds during the post-fledging period may increase their chances of establishing a stable flock, thus making it difficult for transient birds to establish themselves within such flocks. Baeyens (1981) noted that in late summer and early fall stable flocks form with transient individuals moving between flocks, often remaining as solitary individuals over winter. This may have been true of the transients found on this study area as well.

The dominance hierarchy formed, based on agonistic interactions was linear, similar to that described by Baeyens (1981) and Reese and Kadlec (1982). In certain cases encounters among pairs of birds were not recorded, however, by knowing the relationship among most dyads, the ranks of all could be deduced. The hierarchy consisted of 3 adults and 12 juveniles (Table IV-1). The two top-ranking birds were adult males, with the remaining adult, a female, ranked fifth.

After the determination of the dominance hierarchy, I grouped the birds into three dominance categories with the most dominant five birds being categorized as dominant (D), the middle five as intermediate (I), and the bottom five as subordinate (S). Equal numbers of individuals per category were initially chosen because it allowed for easier statistical manipulation and fewer assumptions regarding relative differences in dominance rank among flock members. However, interactions between a male (Rank 4) and a female (Rank 5) suggested that they were pair-bonded. Therefore, I eliminated these two individuals from the analysis. Finally, the number of times two birds fed together was recorded along with the dominance category for which the two belonged (DD, DI, DS, II, IS, SS).

The frequency of associations recorded among birds of various dominance categories suggest that they were not feeding together at random (Table IV-2). The five categories contributing most to the difference were DS and SS (more than expected) and IS and DI (less than expected values). It appears that dominant-subordinate and subordinate-subordinate associations were the most frequent at the feeding station. Marler (1955-57) recorded that subordinate chaffinches fed in closer proximity to one another than dominant birds at a feeding station. He suggested that females had a shorter individual distance which allowed them to feed in close proximity to one another, therefore increasing a subordinate's chance of acquiring food when food was limiting.

Under captive conditions (Chapter III) there was a significant difference in the frequency of aggressive and submissive interactions according to sex; males interacted more aggressively with other males than did females with other females. Interactions between males and females had a similar number of aggressive and submissive outcomes. In this study of free-ranging magpies the frequency of

Table IV-1. The outcome, in terms of wins and losses, of interactions among members of a flock of magpies. Birds are ranked according to the outcome of these interactions, from alpha (bird number 1) to omega (bird number 15). The numbers in the body of the table represent interactions won by birds on the left over birds on top. Age: A=adult, J=juvenile. Sex: M=male, F=female.

	Dominant (D)					Intermediate (I)					Subordinate (S)					Total	
Age	A	A	J	J	A	J	J	J	J	J	J	J	J	J	J		
Sex	M	M	M	M	F	M	?	?	F	F	F	F	F	F	F		
Rank	1	2	3	4	5	6	7	8	9	10	11	[illegible]	[illegible]	14	15	Won	Lost
1	–	5	4	1	3	5	5	1	[illegible]	[illegible]	[illegible]	8	0	4	4	41	0
2	–	–	4	0	5	[illegible]	0	0	3	4	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5
3	–	–	–	4	7	2	0	11	3	2	16	3	[illegible]	[illegible]	[illegible]	59	8
4	–	–	–	–	0	4	4	0	1	5	1	2	0	[illegible]	[illegible]	22	5
5	–	–	–	–	–	2	6	0	0	7	1	3	1	0	4	24	15
6	–	–	–	–	–	–	0	2	2	2	0	0	0	1	1	8	18
7	–	–	–	–	–	–	–	0	10	3	1	3	3	6	1	24	15
8	–	–	–	–	–	–	–	–	4	0	3	5	4	0	5	21	14
9	–	–	–	–	–	–	–	–	–	0	0	0	3	0	3	6	23
10	–	–	–	–	–	–	–	–	–	–	3	1	0	0	3	7	23
11	–	–	–	–	–	–	–	–	–	–	–	1	0	1	2	4	27
12	–	–	–	–	–	–	–	–	–	–	–	–	0	0	2	2	29
13	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	3	19
14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	19
15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	37

Table IV-2. The number of times two magpies from a flock of 15 were seen feeding together at a limited food source. Birds were placed according to dominance rank (Table IV-1), into dominant (D), intermediate (I), and subordinate (S) groups. Expected values were based on the probability of two birds interacting by chance alone and hence reflect the number of possible combinations for each type of dyad.

	DD	DI	DS	II	IS	SS	P[a]	Total
Observed	1	4	9	4	6	10		34
Expected	1	7	7	4	11	4	<0.05	
Difference	0	-3	+2	0	-5	+6		

[a] G-test, G= 11.10

association according to sex suggested a trend that the frequency of associations among females at the feeding station were greater than expected, whereas among male and female birds was similar to values predicted by chance (Table IV-3).

These data on free-ranging magpies indicate that subordinate birds feed together more frequently at a limited food source than any other possible combination but this may be a result of subordinate birds being females and having smaller individual distances when associating with other females. Thus, sex of individuals involved appears to modify the nature of interactions. Additionally dominant and subordinate birds fed together more frequently than dominant-dominant dyads. The first prediction of the behavioral model is supported in the field; namely that birds of low social status are able to gain access to limited food resources because of the tolerance to close approach shown towards them by dominant individuals. Thus, the type of interactions that occur among birds within hierarchies of black-billed magpies are influenced by the dominance status of the birds which, in turn, often reflects their sex.

Table IV-3. The number of times two magpies of a given sex from a flock of 15 seen feeding together at a limited food source. Expected values were based on the probability of two birds interacting by chance alone and hence reflect the possible combination for each type of dyad.

	Male-Male	Male-Female	Female-Female	P[a]
Observed	1	14	17	P= 0.07
Expected	4	16	12	
Difference	-3	-2	+5	

[a] Based on G-test: G=5.33

V. SIZE-DOMINANCE RELATIONSHIPS

Morphological Correlates with Dominance
in the Black-billed Magpie

ABSTRACT

Dominance hierarchies have been reported for wild flocks of black-billed magpies (*Pica pica*). The plumage of male and female magpies is similar (monomorphic). However, differences in size have been recorded both between and within sexes; males generally are larger than females. When birds in flocks of mixed sex are considered, all morphological measurements were positively correlated with dominance. However, this relationship results from males being both dominant to and larger than females. Within a given sex, bill size of males is positively correlated with dominance, whereas in females it is negatively correlated. In addition, the relationship between overall size and dominance status, based on principal component analysis, is positive in males but not in females. Thus, size may be an attribute which influences an individual's potential to attain high dominance status, particularly among males.

INTRODUCTION

The degree of individual morphological variation within species differs among passerines (Rohwer 1975, Shields 1977, Baker and Fox 1978). Rohwer (1975) suggests that variation among individuals may act to signal dominance status and thus reduce intraflock fighting. Thus, an individual's status may be largely predetermined or influenced by its appearance. Consequently one might expect a correlation between morphological characters and dominance status.

Several factors which have been reported to influence dominance status in birds are: age (older birds dominate younger, Hepp and Hair 1984); sex (males dominate females, Balph 1975, Alexander and Hair 1979); plumage coloration (Marler 1955-57, Harrington 1973, Rohwer 1975, Fungle *et.al.* 1984); hormonal level (high titre of circulating testosterone in dominant birds with low titre in subordinates, Noble and Wurm 1946, Watson and Moss 1971, Lumia 1972); and breeding status (paired birds of either sex dominant to unpaired birds, Patterson 1977, Hepp and Hair 1984).

Baeyens (1981) and Scharf (Chapter IV) report that dominance hierarchies are present in flocks of wild magpies (*Pica pica*). The appearance of the plumage in the sexes of magpies is similar; however, differences in size exist both within and between sexes with females being significantly smaller than males (Appendix 2). This study was undertaken to determine whether size is correlated with dominance status of individuals within flocks of juvenile black-billed magpies.

METHODS

Magpies were live-trapped in baited circular-funnel traps (Alsager *al. et.* 1972) during the fall of 1982 and 1983 in the city of Edmonton, Alberta, Canada. Each bird's sex was determined from external measurements (Appendix 2); sex was verified by gonadal examination after the birds were killed at the end of the experiment. All birds were individually color-marked with plastic leg bands, measured with calipers and a steel rule, and placed in outdoor aviaries. The measurements taken are presented in Appendix 4. The aviary flight cages measured 5.8 m x 2.4 m x 2.1 m high and were attached at one end to an enclosed room (2.1 m x 2.4 m x 2.1 m). Each group of birds caught at a given trapping station was placed in a separate cage.

Only juvenile birds were used to eliminate any effects of age. All birds were given 3 weeks to acclimate to the penned conditions before being randomly assigned to pens such that no new members of each new flock of five birds were known to have had previous associations with any other bird.

The dominance status of flock members was assessed by recording, from a blind, the outcomes of agonistic encounters between birds at a centralized food source. A win was scored when one bird either displaced another from the food or caused it to behave in a submissive manner (Baeyens 1979). The results of encounters among all pairs within a given cage enabled me to arrange flock members in a linear dominance hierachy thereby assigning ranks to each bird (Appendix 1).

The relationship between the morphometric characters and dominance rank was determined by using a Spearman rank correlation procedure (Sokal and Rohlf 1981). Because the sample size used to calculate each correlation for a given morphometric variable was small (n=5), minor deviations from complete concordance could lead to large differences in the coefficients calculated, potentially masking a relationship between size and dominance. In order to eliminate this problem, I determined the area under a nomal distribution represented by the normalized sum of all correlations for a given variable (Table V-1). If the area represented 5% or less (the tails of the distribution; $P<0.05$), it can be stated that there is a significant relationship between dominance and the variable in question.

Although a univariate approach can provide information about the relationship between particular morphometric variables and dominance, it does not address the following question: is overall size correlated with dominance? Overall size of an individual can be viewed as a composite of all physical characters. Therefore, I used principle component analysis (PCA) to derive a linear function of all morphometric variables for all birds. Subsequently principal component scores were derived for each bird from the linear function describing the first PC axis (size). Therefore, the PC score for a given bird represents the bird's overall size in contrast to all other birds. By using these PC scores, Spearman rank correlations between overall size and dominance within a given flock can be calculated. These new correlation coefficients were then subjected to the same normalizing procedure as previously mentioned

Table V-1. Derivation of the normal deviate for estimating the probability associated with the combined Spearman rank correlation.

Definition of Symbols

d	Difference between two quantities (expected and observed ranks)
i	Integer used as subscript
N	The size of a group or category
n	Sample size
r_s	Spearman rank correlation coefficient
T	Sum of r_s
V	Variance of r_s
V_o	Variance of T
Z	Normal deviate, standard score
$\sum$	Taking the sum

1. Computation of the Spearman rank correlation coefficient (r_s) for a morphological variable (Zar 1974, p243-245).

$$r_s = 1 - \frac{6 \sum_{i=1}^{N} d^2}{n^3 - n}$$

2. Computation of the sum of all r_s for a given variable (T).

$$T = \sum_{i=1}^{N} r_s$$

Table V-1. continued

3. Computation of the variance of T which is the pooled variance for all r_s.

$$V_o = \sum_{i=1}^{N} V \; r_s$$

or

$$V_o = \sqrt{\sum_{i=1}^{N} \frac{1}{n-1}}$$

4. The normal score (Z), for a given variable, calculated for the sum of T.

$$Z = \frac{T}{V_o} \quad \text{or} \quad Z = \frac{T}{\sqrt{\sum_{i=1}^{N} \frac{1}{n-1}}}$$

5. The Z score is checked against 1.645, which is the cut off for a one-sided test at the 5% probability level($P < 0.05$).

(Table V-1).

RESULTS AND DISCUSSION

The relationships between each morphometric variable measured and dominance status of the captive magpies, when both sexes were examined together, are presented in (Table V-2).

In encounters between males and females, males, which are significantly larger than females, won significantly more often (Table V-3). Therefore, the strong correlation between size and rank (Table V-2) can be largely explained by larger males dominating smaller females. When the size-dominance relationship was examined according to sex, the only significant positive relationship among males was depth of the bill at the nostril (DTBNOS) (Table V-4). However among females the foot (FOOT) was positively correlated with dominance status whereas width of the bill at the nostril (WTBLNS) was negatively correlated with dominance rank (Table V-5). The bill of male magpies may be useful during aggressive interactions. Bill size may be used by male magpies as a signal of dominance status or it may allow birds to individually recognize one another. However, among females bill width was inversely related to dominance and foot (FOOT) was positively correlated with dominance, but it is unclear how the combination of these two variables could be important during aggressive encounters.

Traditionally researchers have used measurements of morphometric attributes such as wing chord, tarsus length, or weight as indicators of size. However in some cases, one measurement may be less informative than a combination of measurements recognized as size indicators. One technique that can provide an index of overall size is principle component analysis (PCA). PCA provides a linear function which explains the maximum amount of variance among all variables. The relationship between dominance and the predicted PC scores shows a positive relationship when sexes are combined (Table V-6). Moreover when the sexes are examined separately, a positive correlation between dominance and size exists among males but not among females (Table V-6).

Table V-2. Spearman rank correlations (r_s) of size (as measured by a particular morphological measurement and dominance status among all individuals in flocks of captive magpies for both sexes.

Cage Number	Sex Ratio[a] (M)[a]	(F)	WINGCH[b]	WINGBR	LTBLCM	LTBLNS	DTBRIC	DTENOS	WTBNOS	TARSUS	[illegible]	WEIGHT
1	1	4	0.103	0.103	0.154	0.633	-0.200	0.564	0.154	0.564	0.872	[illegible]
2	2	3	0.900	0.700	0.800	0.718	0.700	0.900	0.667	0.700	0.400	[illegible]
3	5	0	0.100	0.053	0.200	-0.447	0.800	0.800	-0.500	-0.103	0.500	[illegible]
4	3	2	0.410	0.158	0.462	0.667	-0.900	0.100	0.100	-0.700	0.100	[illegible]
5	3	2	0.500	0.300	0.564	-0.053	0.900	1.000	0.821	0.308	0.700	[illegible]
6	2	3	0.100	0.051	0.500	0.616	0.472	0.667	-0.103	-0.051	0.700	[illegible]
7	2	3	0.821	0.600	0.783	0.671	0.900	0.200	0.500	0.975	0.800	[illegible]
8	2	3	0.000	0.500	0.564	0.359	0.200	0.600	0.700	0.821	0.900	[illegible]
9	2	3	0.671	0.667	0.577	0.700	0.462	0.500	0.300	0.738	0.500	[illegible]
10	2	3	0.051	0.100	0.718	0.975	-0.600	0.600	0.359	0.359	[illegible]	[illegible]
11	2	3	0.700	0.300	0.821	0.616	1.000	0.700	0.800	0.564	[illegible]	[illegible]
12	1	4	0.800	0.667	0.738	-0.100	0.359	0.800	0.264	0.894	[illegible]	[illegible]
13	3	2	0.700	0.300	0.821	0.616	0.700	0.600	1.000	0.901	[illegible]	[illegible]
14	5	0	0.300	-0.051	-0.867	-0.564	-0.316	0.718	-0.100	0.051	0.462	[illegible]
15	5	0	0.974	-0.462	0.949	0.400	1.000	0.800	-0.200	-0.949	1.000	[illegible]
16	4	1	0.600	0.600	0.564	0.224	0.900	0.872	0.300	0.671	0.564	[illegible]
17	0	5	-0.564	-0.564	0.707	0.707	-0.447	0.300	-0.103	-0.821	0.527	[illegible]
T[c]			7.166	4.022	9.055	6.738	5.930	10.721	4.959	5.023	10.94[illegible]	[illegible]
Z[d]			3.479	1.952	4.396	3.271	2.879	5.204	2.407	[illegible]	5.315	[illegible]
P[e]			**	*	**	**	**	**	**	**	**	**

[a] Sex in parentheses: M=male, F=female.

[b] Abbreviations for the measurements and the discription of how they were taken are presented in Appendix 4.

[c] Sum of all r_s

[d] Normal deviate, standard score calculated for the sum of r_s for a given measurement (Table V-1).

[e] *= P <0.05, P <0.01

Table V-3. Outcome of intersexual agonistic encounters among captive black-billed magpies.

1981-82			Wins by		
Cage Number	Males	Females	Males	Females	Difference[a]
1	1	4	4	0	P < 0.01
2	2	3	98	0	P < 0.01
4	3	2	28	5	P < 0.01
5	3	2	31	0	P < 0.01
6	2	3	33	15	P < 0.01
7	2	3	32	0	P < 0.01
Total			226	20	P < 0.01

1982-83			Wins by		
Cage Number	Males	Females	Males	Females	Difference[a]
8	2	3	41	24	P < 0.01
9	2	3	15	14	n.s.
10	2	3	50	22	P < 0.01
11	2	3	51	0	P < 0.01
12	1	4	67	2	P < 0.01
13	3	2	44	17	P < 0.01
16	4	1	18	0	P < 0.01
Total			286	79	P < 0.01

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[a] Based on G-test

Table V-4. Spearman rank correlations (r_s) between size of a given measurement and dominance for males.

Cage Number	Sample Size	WINGCH[a]	WINGBR	LTBLCM	LTBLNS	DTBRIC	DTBNOS	WTBNOS	TARSUS	FOOT	WEIGHT
2	2	-1.000	-1.000	-1.000	-0.100	-1.000	-1.000	----	-1.000	-1.000	[illegible]
3	5	0.100	0.053	0.200	-0.447	0.800	0.800	-0.500	-0.103	0.800	-1.000
4	3	0.000	0.000	0.866	1.000	-0.500	1.000	0.500	-0.500	0.500	-0.500
5	3	-1.000	-1.000	-1.000	0.000	0.500	1.000	1.000	-1.000	-0.500	-1.000
6	2	1.000	1.000	1.000	1.000	1.000	1.000	----	1.000	1.000	1.000
7	2	1.000	1.000	-1.000	-1.000	-1.000	-1.000	-1.000	1.000	-1.000	-1.000
8	2	-1.000	1.000	----	1.000	1.000	1.000	1.000	1.000	1.000	[illegible]
9	2	1.000	1.000	----	1.000	1.000	1.000	1.000	1.000	----	[illegible]
10	2	1.000	-1.000	1.000	1.000	-1.000	1.000	----	----	0.600	[illegible]
11	2	1.000	-1.000	1.000	1.000	1.000	1.000	-1.000	1.000	[illegible]	[illegible]
13	3	0.200	0.633	-0.316	-0.949	0.400	0.200	1.000	[illegible]	[illegible]	[illegible]
14	5	0.300	-0.513	-0.866	-0.564	-0.316	0.712	-0.100	0.051	[illegible]	[illegible]
15	5	0.974	-0.462	0.949	0 400	1.000	0.800	-0.200	-0.949	[illegible]	[illegible]
16	4	-1.000	-1.000	-0.866	0.866	1.000	0.866	0.500	[illegible]	[illegible]	[illegible]
T[b]		2.574	0.365	1.931	4.206	3.584	8.678	2.200	3.165	3.462	[illegible]
Z[c]		0.830	0.118	0.702	1.357	1.253	2.800	0.800	1.080	1.152	[illegible]
P[d]		n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	[illegible]

[a] Abbreviations for the measurements and the discription of how they were taken are presented in Appendix 4.

[b] Sum of all r_s

[c] Normal deviate, standard score calculated for all r_s of a given measurement.

[d] n.s.= not significant, **= $\underline{P} < 0.01$

Table V-5. Spearman rank correlations (r_s) between size of a given measurement and dominance for females.

Cage Number	Sample Size	WINGCH[a]	WINGBR	LTBLCM	LTBLNS	DTBRIC	DTBNOS	WTBNOS	TARSUS	FOOT	WEIGHT
1	4	-0.316	-0.316	-0.316	0.316	-0.800	0.316	-0.738	0.316	0.949	[illegible]
2	3	1.000	1.000	0.500	0.500	1.000	1.000	-0.500	1.000	1.000	1.000
4	2	1.000	-----	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000	-1.000
5	2	-1.000	1.000	-----	-1.000	1.000	1.000	-1.000	-1.000	1.000	1.000
6	3	-0.500	-0.866	-0.500	-0.500	-1.000	-0.866	-.0500	-1.000	1.000	1.000
7	3	0.000	-1.000	-----	0.866	1.000	-0.500	-1.000	0.866	0.500	-1.000
8	3	0.500	1.000	1.000	0.000	-0.500	0.500	0.500	1.000	1.000	1.000
9	3	-----	0.000	-----	0.500	0.000	-0.500	-1.000	0.866	0.500	-0.866
10	3	-0.866	-0.500	0.500	0.866	-0.500	0.500	0.500	0.500	0.500	0.500
11	3	0.500	0.500	0.000	0.000	1.000	1.000	0.500	0.500	0.500	0.500
12	4	0.500	0.500	0.000	-1.000	-0.500	0.500	0.000	-----	0.500	-0.500
17	5	-0.564	-0.564	0.707	0.707	-0.447	0.300	-0.103	-0.821	0.527	0.100
T^b		0.254	0.754	0.891	0.255	-0.747	3.250	-4.341	1.227	6.976	1.734
Z^c		0.105	0.323	0.424	0.101	0.295	1.285	-1.716	0.491	2.757	0.655
P^d		n.s	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	**	n.s.

[a] Abbreviations for the measurements and the discription of how they were taken are presented in Appendix 4.

[b] Sum of all r_s

[c] Normal deviate, standard score calculated for all r_s of a given measurement.

[d] n.s.= not significant, *= $\underline{P}$ <0.05, **= $\underline{P}$ <0.01

Table V-6. Spearman rank correlation (r_s) of size (as predicted by Principal Component Analysis) and dominance for both sexes combined and separate.

	Combined Sexes	Males	n	Females	n
Cage Number					
1	0.500	-----	1	0.200	4
2	0.700	-1.000	2	1.000	3
3	0.900	0.900	5	-----	0
4	0.100	0.500	3	-1.000	2
5	0.800	0.500	3	-1.000	2
6	0.200	1.000	2	-0.500	3
7	0.600	-1.000	2	0.250	3
8	0.700	1.000	2	1.000	3
9	0.700	1.000	2	0.500	3
10	0.500	-1.000	2	0.500	3
11	0.500	1.000	2	-0.500	3
12	0.700	-----	1	-0.500	4
13	0.900	1.000	3	1.000	2
14	-0.400	0.300	5	-----	0
15	0.000	0.700	5	-----	0
16	0.800	1.000	4	-----	1
17	0.000	-----	0	0.000	5
T^a	8.200	5.900		0.950	
Z^b	3.981	1.900		0.349	
P^c	< 0.01	< 0.05		n.s.	

[a] Sum of all r_s

[b] Normal deviate, standard score calculated for all r_s (Table V-1).

[c] n.s.= not significant

In monomorphic species such as the magpie, variation in size may signal the potential success of an individual when engaging in an aggressive encounter. Fighting has been demonstrated to be costly especially if it results in injury (Chapter II). Injured birds were unable to maintain their weight during periods of food deprivation and hence died. Therefore, signals that may express dominance or facilitate individual recognition are likely to evolve if they increase an individual's fitness.

Clearly large body size would be an advantage during an encounter with a smaller conspecific. Dominance has come to mean priority of access to limited resources (Kaufmann 1983), and dominant birds stand to gain an advantage if the obtained resources have an impact on their individual fitness. However the most perplexing results are that females show little or no relationship of morphology with dominance. Possibly female birds are following a different behavioral strategy within dominance hierarchies.

VI. SIZE DIMORPHISM

Overwinter Changes in Sexual Size Dimorphism in the Black-billed Magpie

ABSTRACT

Dominance is related to the size of males in captive flocks of black-billed magpies (*Pica pica*). Experiments suggest that birds of intermediate size lose more weight during periods of food deprivation than birds at either end of the dominance hierarchy. A model based on behavior observed during the periods of food deprivation predicts that: 1) the proportion of males in the smaller size classes will be reduced in number producing an increase in the mean size of males that survived the winter, and 2) because there is no correlation between size and dominance status for females, there should be little change in the mean size of females that survived the winter. The overall result of this prediction would be to increase sexual size dimorphism among overwintered adult magpies. This study tested these predictions by examining external measurements of juvenile and adult populations of magpie. The results indicate that small males either succumb or disappear overwinter, but females do not. Thus, these results support the prediction of the behavioral model.

INTRODUCTION

Throughout the winter, particularly in the northern parts of the magpie's range, snow cover remains for long periods of time restricting access to scarce winter food resources. During this time black-billed magpies (*Pica pica*) form winter flocks composed primarily of juvenile birds (young of the year) with a few adults (Linsdale 1937, Baeyens 1981, Tatner 1982, Chapter IV). In captive flocks of magpies, size is positively correlated with dominance in males, and, since males are larger than females, they are also dominant to females (Chapter V). Additional food deprivation experiments showed that captive magpies of intermediate size lost proportionally more weight when food was limiting than did birds at either end of the dominance hierarchy (Chapter II). If birds of intermediate rank and size succumb during periods of food deprivation two predictions can be made: 1) the proportion of males in the smaller size classes will be reduced in number producing an increase in the mean size of males remaining in the overwintered population, and 2) because there is no correlation between size and dominance among females (Chapter V), there should be little change in the mean size of females that survive the winter. The overall result should increase sexual size dimorphism among overwintered magpies. In this chapter, I examine these predictions.

METHODS

A total of 214 black-billed magpies was collected throughout the City of Edmonton, Alberta, using circular funnel traps (Alsager *et. al.* 1972), and monofilament snares (Appendix 3), and through shooting by the Division of By-Law Enforcement, City of Edmonton. Young of the year (juveniles) were collected between October and January of 1982 and adult birds (those that were at least 1 year old and had undergone at least one complete molt) were collected throughtout 1982-1983. Age and sex were determined by techniques outlined in Appendix 2; sex was verified by gonadal examination of the carcasses. From each magpie 14 measurements (Appendix 4) were taken, of which nine were used ~~in this~~ study.

Data from four categories (juvenile and adult, male and female) were analyzed by using PCA (Principal Components Analysis), and DFA (Discriminant Function

Analysis)(Rising 1973, Murphy 1978, Johnston and Fleischer 1981), and Fleischer (1981) who examined overwinter changes in sexual size dimorphism of the house sparrow (*Passer domesticus*) and who used principal component analysis and discriminant function analysis (Sneath and Sokal 1973).

RESULTS AND DISCUSSION

The mean values for the nine measurements are presented in Table VI-1. Among females seven of the nine measurements from juvenile birds are larger (but only one significantly so) than those of adults. Among males six of nine measurements are larger in adults than juveniles. Individuals comprising the overwintered adult population appear to have increased the degree of size dimorphism, with adult males being larger and adult females being slightly smaller than in those populations of juveniles measured before the winter.

One way to quantify the change in size dimorphism is to examine the means of all nine measurements concurrently and determine whether the difference between the sexes changes when one compares juvenile and adult samples. The F-test associated with the Mahalanobis (D^2) statistic (a measure of the relative distance between group means) can provide such a test (Morrison 1976). The distance between males and females in the juvenile cohort is 6.91 (D^2), a significant difference (F=18.46, df=9,91, $P< 0.00$), however, among adults the distance has increased to 15.05 (D^2) (F=32.46, df=9,97, $P< 0.00$). Thus, these data support the idea that there was an increase in overwinter sexual size dimorphism. The prediction, based on the behavioral model, namely that the proportion of males in the smaller size classes would be reduced in number through the disappearance of smaller individuals to produce an increase in the mean size of males remaining in the overwintered population, is supported.

An alternative explanation for the observed increase in size dimorphism is that males continue to grow throughout their first winter reaching their determined growth at a later date than females. That would explain why adult males are larger than juvenile males.

In order to examine the validity of this potential explanation, I determined the date at which the upper asymptote for the growth curves of all measurements was

Table VI-1. The means and standard deviations for nine measurements used in analyzing overwinter changes in the size of the black-billed magpie.

	Female					Male				
	Juvenile n=62		Adult n=36			Juvenile n=45		Adult n=71		
Measurement	$\bar{x}$	s.d.	$\bar{x}$	s.d.	Difference[a]	$\bar{x}$	s.d.	$\bar{x}$	s.d.	Difference[a]
wing chord	196.5	5.8	196.3	3.7	n.s.	204.8	5.2	208.0	4.4	$\underline{P} < 0.01$
breadth of the wing	159.3	6.6	159.1	4.6	n.s.	166.8	5.7	169.1	7.0	$\underline{P} < 0.05$
length of the bill at the gape	40.6	2.1	41.1	1.8	n.s.	43.5	1.0	44.1	1.6	$\underline{P} < 0.05$
length of the bill from nostril to tip	24.9	3.3	24.4	1.5	n.s.	26.2	1.2	26.5	1.7	n.s.
depth of bill at the gape	13.3	0.6	13.3	0.5	n.s.	14.3	0.6	14.4	0.6	n.s.
depth of bill at the nostril	12.5	0.5	12.7	0.4	n.s.	13.7	1.0	13.8	0.5	n.s.
width of bill at the nostril	11.8	0.9	11.5	0.9	n.s.	12.6	1.0	12.5	1.0	n.s.
tarsometatarsus	48.0	2.7	46.6	2.6	$\underline{P} < 0.05$	50.5	1.8	50.5	2.3	n.s.
foot	73.4	2.8	73.2	3.0	n.s.	77.5	2.6	77.3	3.8	n.s.

[a] Based on t-test: n.s.= not significant

achieved. This was done by fitting the best logistic curve to the growth pattern of nestlings recorded during the summer of 1982 (derivative free non-linear regression model, BMDP Program LR, 1983). The structure which took the longest time to reach its asymptotic value was the length of the bill from the nostril to the tip of the upper mandible; this was on July 11, well before the time the juvenile sample was collected (October) (Table VI-2).

These measurements suggested that definitive size was achieved by the end of the summer (July) in the magpie's first year. However this method is indirect and a more appropriate way to determine whether growth continues is to measure the same individual in its first and second year. Measurements recorded from captive birds first measured as juveniles and then again as adults are presented in Table VI-3. Captive juvenile birds in this sample were measured on October 16, 1982, then again as adults on November 3, 1984. These data indicated that the lengths of the wing chord and the breadth of the wing were significantly larger as adults than as juveniles for both sexes, implying that development continued past the first year. However, when the measurements were taken on October 16, 1982 feather abrasion was noted on the primaries and secondaries, presumably a result of the young birds brushing their remiges against the sides of the enclosure when clinging to the wire cage. Consequently the changes in feather length may be largely a function of feather wear after the birds were first caged and should be questioned.

The procedures previously used to detect overwinter changes in size were re-examined. This time the wing measurements were excluded from the data set. Under these conditions ,the Mahalanobis distance between juvenile males and females in fall was $D^2=6.66$ ($F=23.34$, df=7,99, $P<0.01$) and in spring $D^2=9.39$ ($F=26.53$, df=7.93, $P<0.01$). Thus, a significant difference existed between males and females in the juvenile cohort (fall) and this difference was even greater when the adult cohort (spring) was examined. Therefore it appears that an increase in size dimorphism has occurred.

An additional way to examine changes in size is by using principal components analysis because PCA determines an axis indicative of size and as a result PC scores can be calculated which can be used to test for differences among adults and

Table VI-2. Date at which the growth of a given measurement reached its asymptotic value for black-billed magpie nestlings in 1982.

Measurement	Date[a]	
	Males n=9	Females n=13
wing chord	July 3	June 28
breadth of the wing	no data	no data
length of bill at the gape.	June 27	June 29
length of bill from nostril to tip	July 7	July 11
depth of bill at the gape	July 7	June 25
depth of bill at the nostril	July 10	July 5
width of bill at the nostril	June 10	June 8
tarsometatarsus	May 24	May 27
foot	May 28	May 29

[a] The date was predicted by fitting the best logistic growth curve through the growth pattern exhibited by nestlings. The number of days it took the structure to grow to its asymptotic value was advanced from the mean hatch date (April 24), thus, the date given is only an estimate.

Table VI-3. Comparison of 9 measurements on the same birds measured first as juveniles then as adults.

	Female					Male				
	Juvenile n=6		Adult n=6			Juvenile n=4		Adult n=4		
Measurement	$\bar{x}$	s.d.	$\bar{x}$	s.d.	Difference[a]	$\bar{x}$	s.d.	$\bar{x}$	s.d.	Difference[a]
wing chord	189.2	4.1	196.8	2.6	$P < 0.01$	201.5	3.9	205.8	3.1	$P < 0.01$
breadth of the wing	154.0	3.0	159.3	4.4	$P < 0.01$	162.3	5.5	168.0	3.5	$P < 0.05$
length of the bill at the gape	40.3	0.8	40.2	1.5	n.s.	44.0	0.8	43.3	1.0	$P < 0.05$
length of the bill from nostril to tip	24.0	1.0	23.0	2.1	n.s.	25.8	0.5	25.8	1.5	n.s.
depth of bill at the gape	12.3	0.4	12.4	0.3	n.s.	13.9	0.6	13.4	1.0	n.s.
depth of bill at the nostril	12.0	0.4	12.0	0.4	n.s.	13.2	0.6	13.1	0.6	n.s.
width of bill at the nostril	11.9	0.6	11.4	0.3	n.s.	13.1	0.7	13.1	0.6	n.s.
tarsometatarsus	47.8	2.6	47.2	1.9	n.s.	50.5	3.9	48.8	3.3	$P < 0.05$
foot	72.8	1.8	71.7	3.5	n.s.	no data				

a- Based on Paired t-test: n.s.= not significant juveniles according to sex (Table VI-4). These data indicate a trend for larger males to be found in the spring population than in the fall. Additionally by using a two-way discriminant analysis a further examination of the change in size overwinter can be done whereby both age classes are categorized according to sex on the basis of size. As a result of this analysis the overlap between juvenile male and female birds in the fall was recorded at 11%, however, in the spring it had been reduced to 7%. Additionally, the canonical group centroids, which describe the mean size of birds for a given sex and age class, indicated that adult males are larger than juvenile males (1.30 vs. 1.05) and that adult females are smaller than juvenile females (-1.54 vs.-1.47). Although this new set of analyses did not incorporate feather measurements, it does suggest that overwinter size dimorphism does increase.

Overwinter sexual size dimorphism has been reported to occur in the house sparrow (Bumpus 1899, Rising 1973, Murphy 1980, Johnston and Fleischer 1981). Johnston and Fleischer (1981) showed that the degree of overlap in a series of skeletal measurements for males and females was greater in fall than spring. It was suggested that overwinter mortality of small males and large females left the larger males and smaller females to form the spring population, thus increasing overwinter sexual size dimorphism among birds. A question that arises is whether the skeletal structure of male birds continues to grow overwinter? At the present time I am unaware of any literature that examines determinate growth in skeletal measurements of the house sparrow. However if skeletal measurements do not increase after a bird's first winter, then selective mortality increasing size dimorphism overwinter is implied. If sexual size dimorphism can be clearly demonstrated in magpies on the basis of skeletal measurements, it would still remain to be determined whether external meaurements are highly correlated to internal ones. Only then could the behavioral model be invoked as a causal mechanism influencing the increase in sexual size dimorphism among overwintered birds.

Table VI-4. Changes in the mean values (PC scores) predicted by the first principal component (overall size) between juveniles and adults of both sexes of the black-billed magpie.

	Female		Male	
	Juvenile n=62	Adult n=36	Juvenile n=45	Adult n=71
Mean	-0.921	-0.854	0.775	0.919
s.d.	0.652	0.562	0.350	0.471
Difference[a]	n.s.		$P < 0.10$	

[a] Based on t-test: n.s.= not significant

VII. GENERAL DISCUSSION

Flocking of conspecifics, a form of social behavior, can have important implications for the fitness of individual flock members. Two hypotheses have been suggested to explain the adaptive significance of flocking behavior. One suggests that predator detection through group vigilance and signals by flock members warns others of the presence or approach of a predator (Powell 1974, Caraco *et. al.* 1980, Pulliam and Millekan 1982). The second suggests that foraging success of a flock member is enhanced through the ability of the flock to find patchily distributed food sooner and with greater regularity than can a single bird (Powell 1974, Pulliam and Millekan 1982). As a consequence, an individual bird benefits more by flocking than living alone. However, within flocks asymmetries in dominance status among individuals establishes an order of precedence that can influence a given bird's access to a limited resource such as food. Consequently, flock members stand to receive a benefit from flocking, although all members potentially do not receive the same benefit.

Schjelderup-Ebbe (1922) originally defined dominance on the basis of outcomes of agonistic interactions between individuals. Initial research on this suject focused on the documentation of dominance in various species (Evans 1936, Maslow 1940, Gauthreaux 1978); more recently, considerable attention has been focused on the role played by dominance in access to resources. Hence dominance has been defined on a functional basis; dominant birds gain priority of access to a given resource. This definition has enabled researchers to make specific predictions such as that recently proposed by Gauthreaux (1978). He predicted that differential migration in birds is influenced by dominance such that dominant birds gain priority of access to preferred winter habitats, forcing subordinate birds to reside in less favorable habitats. Thus dominant birds survive better than subordinate birds, and therefore are more likely to have greater individual fitness.

Fitness is not only difficult to measure but it is often difficult to substantiate that dominance confers priority of access to a given resource, an issue that has received considerable debate among non-human primate researchers (Gartlan 1968, Bernstein 1970, Rowell 1974). A key measure of an individual's fitness is whether it survives to reproduce (Arnold and Wade 1984a, 1984b). If dominance influences survival, conventional wisdom would predict that dominant birds, when faced with a period of food limitation, should survive better than subordinate birds.

Work done by Fretwell (1969) indicated that subordinate, individually-marked dark-eyed juncos are less likely to be recaptured overwinter because they disperse or die. Kikkawa (1980) demonstrated that subordinate birds in a marked population of silvereyes had lower survival over the non-breeding season than dominant birds. More recently, a study by Baker and Fox (1981) on captive dark-eyed juncos indicated that when the weight of birds fell to approximately 17 grams, death was imminent. Since female juncos weigh less than males (Ketterson and Nolan 1983), and females are also subordinate (Balph 1975), it is more probable that females reach 17 grams before males. Hence, it is likely that females face starvation sooner than males. These data have been interpreted to support the contention that survival is inversely related to dominance.

Magpies in the northern part of their North American range are subjected to severe winter conditions during which food resources are likely to be limiting. Birds with territories spend a considerable amount of time on their territories in winter, presumably using food cached there during the fall (Hochachka pers. comm., Trost pers. comm.). Territorial adults apparently have a much lower rate of disappearance than non-territorial birds which have not yet formed pair-bonds or established territories (Scharf unpublished). However, juveniles form flocks overwinter moving about in areas unsettled by adult territorial birds (Baeyens 1979, 1981). It is within these flocks that dominance-induced mortality should be observed. I have tested whether dominance influences survival as measured by the proportional amount of weight lost during periods of food deprivation of captive flocks of juvenile black-billed magpies.

Data presented herein (Chapter II) indicate that birds of low social status (subordinate birds) are able to gain access to limited food resources. A model based on behavioral observations during the deprivation experiments suggest that dominant birds tolerate the close approach of low-ranking birds and as a result low-ranking birds gain access to food. The outcome is a greater weight loss for intermediate-ranked birds than either dominant or subordinate birds.

Similar behavior patterns have has been observed for other species. Lorenz (1938) recorded that within flocks of semi-tame jackdaws low-ranking female birds were allowed access to restricted food sources by top ranking dominant males. He also noted that top-ranking males often paired with low-ranking female birds with the pair often acting cooperatively in defense of a resource. On occasion a dominant male would intervene on behalf of his mate or prospective mate when the female was interacting with another bird. Craig *et. al.* (1982) observed in flocks of Mexican jays (*Aphelcoma ultramarina*) that certain dominant birds, having gained control of a food source, allowed subordinate birds, access to it. These subordinate birds had a lower variance in food intake than birds that were higher in rank. Similar obserations have been recorded for magpies in the aviary (Chapter III, Reebs pers. comm.). In order to understand the nature of this behavior among magpies, I attempted to quantify the types of agonistic interactions occurring among flock members.

Data collected on the time two birds spent together at a food source indicate that birds that differ greatly in dominance status spent a significantly longer time foraging together than birds similar in rank (Chapter III). The time spent by a given individual at a food source indicated that subordinate birds spent more time feeding together than birds of intermediate rank (Chapter III). Behavior observed during this time indicated that dominant birds, after gaining control of the food source, allowed subordinate low-ranking birds access to it. Similar results were obtained when examining the frequency of feeding associations in a wild flock of 15 birds (Chapter IV). For asymmetries to develop in the response of one bird to others in the flock, magpies must be able to recognize one another as individuals.

Marler (1955-1957) determined that chaffinches respond to visual cues such as plumage characteristics. Females with breast feathers dyed, to imitate the male plumage won a greater proportion of agonistic encounters with normal undyed females. Furthermore when the lowest bird in an established female flock was dyed its dominance status rose through an increase in the number of encounters it won. Marler (1955-57: 144) stated that the red breast acts as a releaser: "a character peculiar to an individual of a given species and to which responsive releasing mechanisms of conspecific individuals react and thus set in motion definite chains of instinctive actions."

On a more refined level Rohwer (1975) examined plumage variability in terms of its adaptive significance. He determined that an individual's dominance may be largely influenced by its appearance. Therefore it should be expected that a correlation between morphological characters and dominance status would exist. In evaluating this hypothesis in magpies, I determined that overall size is correlated with dominance in males but not in females (Chapter V). If size were a signal of dominance, and dominance allowed priority of access to a given resource, then the positive relationship between size and dominance status in males should indicate that males are competing for resources. Such resources could be food, potential territories and/or potential mates.

If the behavioral model reflects events occurring among free-ranging magpies, two predictions can be made: 1) the proportion of males in the smaller size classes will be reduced in number through competiton, producing an increase in the mean size of males remaining in the overwintered population, and 2) because there is no correlation between size and dominance among females there should be little change in the mean size of females in the overwintered female population. I tested these predictions by examining the changes in size of external characters of a juvenile ~~and~~ adult population of black-billed magpies. The results suggested that sexual size dimorphism did, in fact, increase in the overwinter population. Other studies have documented such increases in sexual size dimorphism overwinter such as in the house sparrow, another northern resident bird. Bumpus (1899) concluded that during periods of harsh winter weather females were subjected to stabilizing selection and males to directional selection for larger size (Johnston et. al. 1972). Since then Bumpus' data have been reevaluated using multivariate statistics (Johnston *et. al.* 1972, Rising 1972) and the hypotheses confirmed. Johnston and Fleischer (1981) subsequently examined fourteen skeletal measurements taken from two samples, one collected before and one after the winter. They also recorded an increase in sexual size dimorphism in the overwintered population. They suggested that "birds of intermediate size are at a competitive foraging disadvantage under conditions of persistent snow cover" (Johnston and Fleischer 1981:503). Fleischer and Johnston (1984:409) concluded that "lowered aggression reduced energy requirements and a greater choice in roosting cavities increasing the survivorship of smaller females. Likewise, behavioral dominance by large males combined with thermoregulatory advantages may result in selection for males of large size. Overall multiple selective pressures can combine to produce the same direction of selection, and, for each sex, different selective mechanisms (or combinations of mechanisms) may act." These data for house sparrows and the interpretation used to explain the increase in size dimorphism among overwintered birds are similar to that predicted by the behavioral model for magpies. As a result the behavioral model may reflect the mechanisms which influence overwinter size dimorphism.

One additional approach to understand better the behavioral model in terms of an individual's net energy budget is to devise a simulation based on empirical data. The simulation presented here is based on the behavioral model (Chapter II); it quantitatively examines energy uptake (tolerance to approach of another bird and hence its access to food) and energy expenditure (loss of energy resulting from the intensity and frequency of agonistic encounters). In this simulation each member of a flock of a given rank receives a payoff reflecting the net benefit resulting from gaining access to food and the cost suffered by expending energy as a consequence of interacting with all other individuals.

The rules of the simulation are as follows:

Benefits

I used a curve describing the relationship between the difference in rank of two individuals and the time spent feeding together (Chapter III, Figure III-1) as an index of their net energy gained. However, to simplify matters I have re-scaled the Y-axis downward by a magnitude of ten for ease of calculation (Figure VII-1). In addition, the dominant bird of a interacting dyad received an added benefit (+1) regardless of its actual rank because it is obvious that the dominant bird under these conditions receives greater benefit than the subordinate.

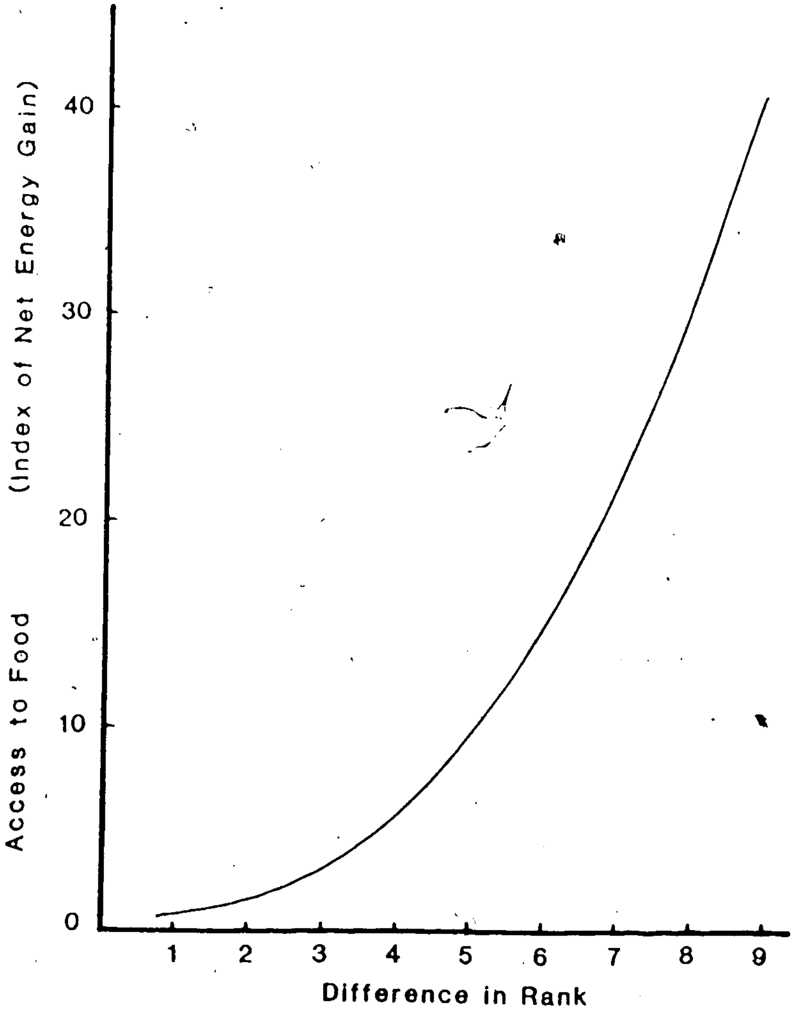

Figure VII-1. Relationship between access to food as influenced by the difference in rank of two magpies (based on data presented in Chapter II, Figure III-1). The segment of the curve beyond a difference in a rank of 4 has been extrapolated from the equation of that line ($y= 18.5-19.0\,x + 6.89\,x^2$).

Costs

Because I have no data to express the relationship between energy expended during an encounter and a bird's difference in rank, I have assumed a negative linear relationship of "likes will fight" (Geist 1966, 1971, Figure VII-2).

The payoff received by each bird reflects both the cost and benefit an individual receives as a result of interacting at random with all individuals in a flock (Table VII-1). The payoff matrices for flocks of 3, 5, 7 and 10 individuals are presented in Tables VII-2 and, VII-3 (Figures VII-3, VII-4). The payoffs indicate that dominant and subordinate birds of flocks of 3 and 10 magpies receive the greatest benefit from their association within the flock whereas birds intermediate in social status receive less. This pattern is the same regardless of flock size within the limits imposed. If one holds costs constant across all ranks and considers only benefits, the net payoffs again indicate that dominant and subordinate birds receive greater benefits from their association than birds of intermediate rank (Figure VII-4). In either case the predictions of the behavioral model are supported.

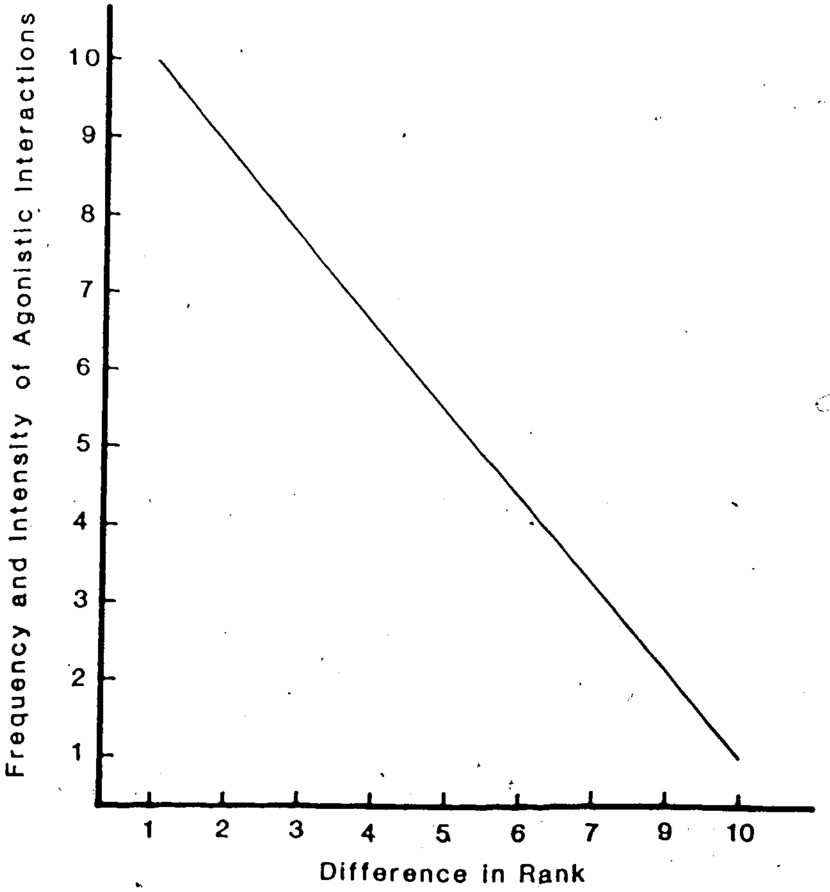

Figure VII-2. The relationship between the frequency and intensity of interactions between two magpies and their difference in rank. This relationship is based on "likes will fight" (Geist 1971).

Table VII-1. Payoff schedule (benefit+costs) for magpies according to their difference in rank.

Difference in Rank	Benefits[a]	Costs[b]	Payoffs for	
			Dominant (+1)[c]	Subordinate
1	0.6	-10.0	-8.4	-9.4
2	0.8	-8.8	-7.0	-8.0
3	2.4	-7.7	-4.3	-5.3
4	5.3	-6.6	-0.3	-1.3
5	9.6	-5.5	5.1	4.1
6	15.3	-4.4	11.9	10.9
7	22.3	-3.3	20.0	19.0
8	30.8	-2.2	29.6	28.6
9	40.6	-1.0	40.6	39.6

[a] Data taken from Figure VII-1.

[b] Data taken from Figure VII-2

[c] The dominant bird receives greater benefit, arbitrarily set at +1 (see text)

Table VII-2. Matrices of payoffs received by birds according to rank when both benefits and costs are summed (A) and when benefits alone are considered (B). Payoffs are based on the assumption that all birds interact with one another at random. Dominance rank: 1=most, 10=least.

A Benefits+costs

	Dominance Rank										
	1	2	3	4	5	6	7	8	9	10	Payoff
1		-8.4	-7.0	-4.3	-0.3	5.1	11.9	20.0	29.6	40.6	87.2
2	-9.4		-8.4	-7.0	-4.3	-0.3	5.1	11.9	20.0	29.6	37.2
3	-8.0	-9.4		-8.4	-7.0	-4.3	-0.3	5.1	11.9	20.0	-0.4
4	-5.3	-8.0	-9.4		-8.4	-7.0	-4.3	-0.3	5.1	11.9	-25.7
5	-1.3	-5.3	-8.0	-9.4		-8.4	-7.9	-4.3	-0.3	5.1	-38.9
6	4.1	-1.3	-5.3	-8.0	-9.4		-8.4	-7.9	-4.3	-0.3	-39.9
7	10.9	4.1	-1.3	-5.3	-8.0	-9.4		-8.4	-7.9	-4.3	-28.9
8	19.0	10.9	4.1	-1.3	-5.3	-8.0	-9.4		-8.4	-7.9	-5.4
9	28.6	19.0	10.9	4.1	-1.3	-5.3	-8.0	-9.4		-8.4	30.2
10	39.6	28.6	19.0	10.9	4.1	-1.3	-5.3	-8.0	-9.4		78.1

B Benefits

	1	2	3	4	5	6	7	8	9	10	
1		0.7	0.9	3.4	6.3	10.6	16.3	23.3	31.8	41.6	134.9
2	0.6		0.7	0.9	3.4	6.3	10.6	16.3	23.3	31.8	93.9
3	0.8	0.6		0.7	0.9	3.4	6.3	10.6	16.3	23.3	62.9
4	2.4	0.8	0.6		0.7	0.9	3.4	6.3	10.6	16.3	42.0
5	5.3	2.4	0.8	0.6		0.7	0.9	3.4	6.3	10.6	31.0
6	9.6	5.3	2.4	0.8	0.6		0.7	0.9	3.4	6.3	30.0
7	15.3	9.6	5.3	2.4	0.8	0.6		0.7	0.9	3.4	39.0
8	22.3	15.3	9.6	5.3	2.4	0.8	0.6		0.7	0.9	57.9
9	30.8	22.3	15.3	9.6	5.3	2.4	0.8	0.6		0.7	87.8
10	40.6	30.8	22.3	15.3	9.6	5.3	2.4	0.8	0.6		127.7

Table VII-3. Net payoffs received by birds according to flock size and dominance status, when both benefits and costs are summed (A) and when benefits alone are considered (B). Payoffs are based on the assumption that all birds interact with one another at random.

A Benefits+costs	Flock Size			
Dominance Rank	3	5	7	10
1	-15.4	-20.0	-2.4	87.2
2	-17.8	-29.1	-24.3	37.2
3	-17.4	-32.8	-37.4	-0.4
4		-31.1	-42.4	-25.7
5		-24.0	-39.4	-38.9
6			-28.3	-39.9
7			-9.0	-28.7
8				-5.4
9				30.2
10				78.2
B Benefits				
1	1.6	11.3	38.2	138.9
2	1.3	5.6	22.5	93.9
3	1.4	3.0	12.7	62.9
4		4.5	8.8	42.0
5		9.1	10.7	31.0
6			19.4	30.0
7			34.0	39.0
8				57.9
9				87.8
10				127.7

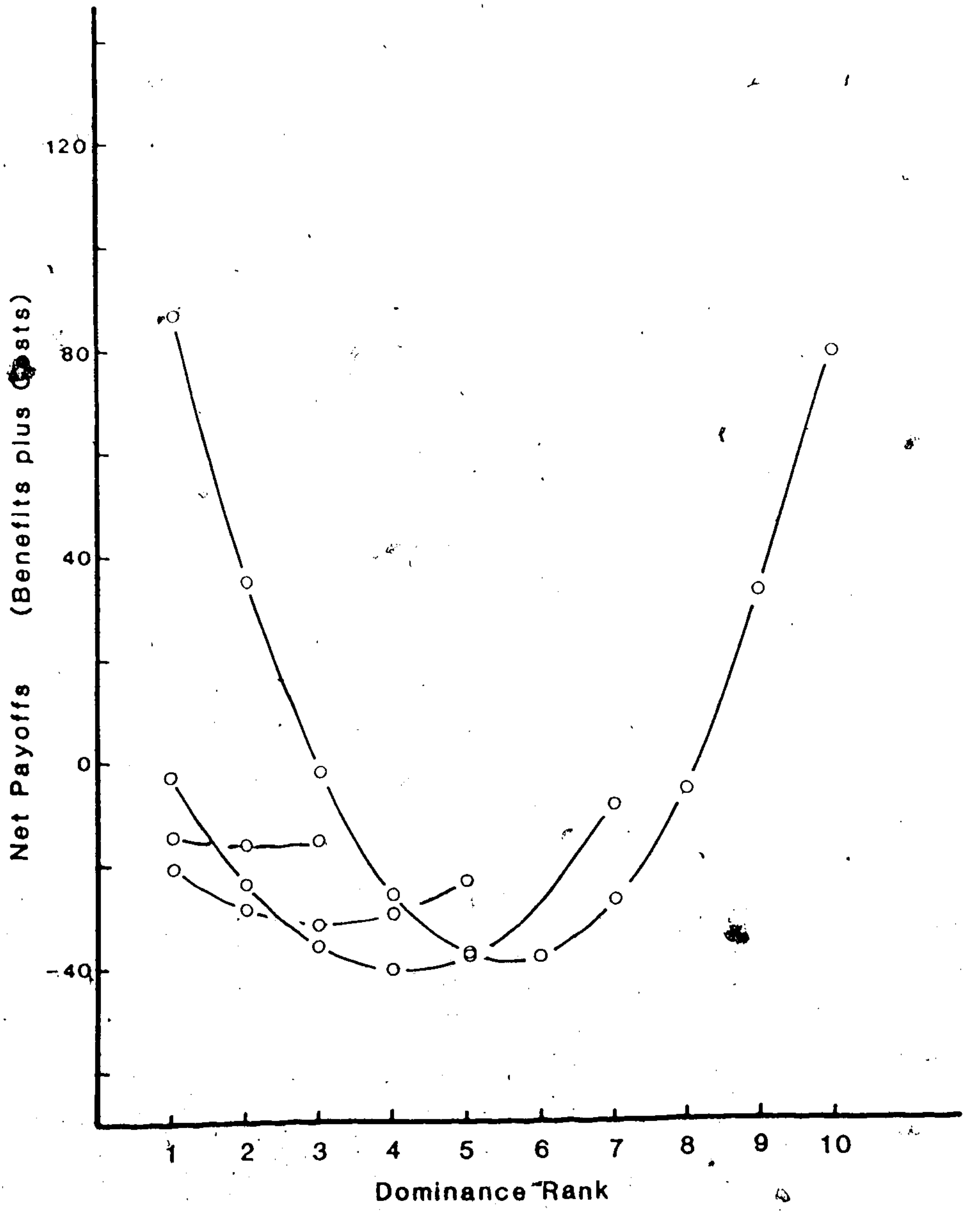

Figure VII-3. Plot of the net payoffs (benefits+costs) to birds according to their rank (1=alpha, 10=omega).

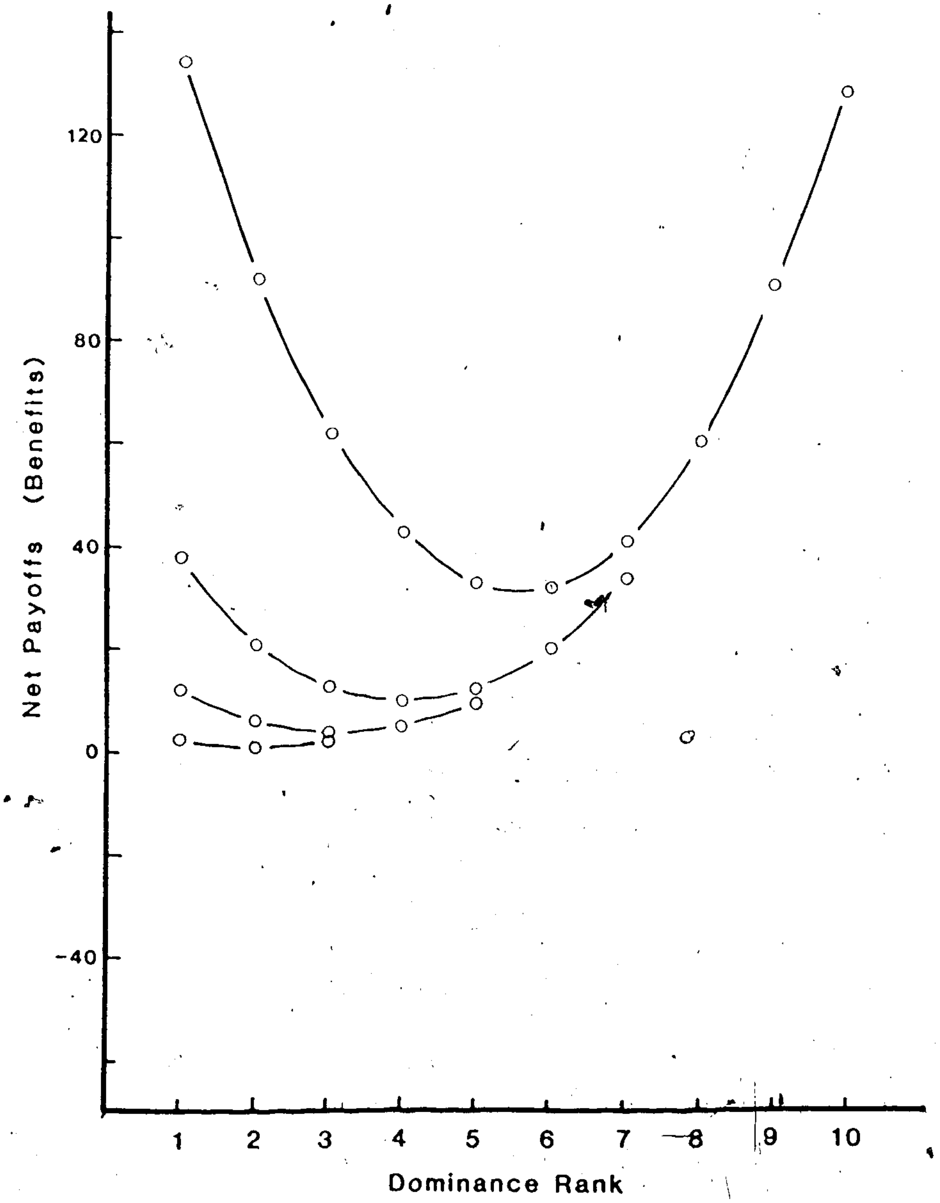

Figure VII-4. Plot of the net payoffs (benefits only) accrued by birds according to their rank (1=alpha, 10=omega).

VIII. LITERATURE CITED

Alexander, R.D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst., 5:325-383.

Alexander, W.C., and J.D. Hair. 1979. Winter foraging behavior and aggression of diving ducks in South Carolina. Proc. Ann. Conf. Southeast. Assoc. Game Fish. Comm., 311:226-232.

Alsager, D., J. Stenrue, and R. Boyles. 1972. Capturing black-billed magpies with circular live traps. J. Wildl. Manage., 36:981-983.

Appleby, M.C. 1983. The probability of linearity in hierarchies. Anim. Behav., 31:600-608.

Arnold, S.J., and M.J. Wade. 1984a. On the measurement of natural selection: applications. Evolution, 38:709-719.

----------. 1984b. On the measurement of natural selection: theory. Evolution, 38:720-734.

Baeyens, G. 1979. Description of the magpie (*Pica pica*). Ardea, 67:28-41.

----------. 1981. Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. Ardea, 69:145-166.

Baker, M.C., and S.F. Fox. 1978. Dominance, survival, and enzyme polymorphism in dark-eyed juncos (*Junco hyemalis*). Evolution, 32:697-711.

Balph, M.H. 1975. Wing length, hood coloration, and sex ratio in dark-eyed juncos wintering in northern Utah. Bird-Banding, 46:126-130.

Bancroft, G.T., and A.E. Woolfenden. 1982. The molt of scrub jays and blue jays in Florida. Ornithological Monograph, 29:1-51.

Berger, D.D., and H.C. Mueller. 1959. The bal-chatri: a trap for the birds of prey. Bird-Banding, 30:18-26.

Bent, A. 1946. Life histories of North American Birds. U.S. National Museum Special Bull., No. 191.

Bernstein, I.S. 1970. Primate status hierarchies. *In*. Primate Behavior. (L.A. Rosenblum, ed.). Academic Press, New York, New York.

Bertram, B.C.R. 1978. Living in groups: *In*, Behavioural Ecology, an Evolutionary Approach. (J.R. Krebs, and N.B. Davies, eds.). Sinauer, Sunderland, Mass.

Birkhead, T.R. 1979. Mate guarding in the magpie (*Pica pica*). Anim. Behav., 27:866-874.

----------. 1982. Timing and duration of mate guarding in magpies (*Pica pica*). Anim. Behav., 30:277-283.

Brown, J.L. 1963. Aggressiveness, dominance and social organization in the Steller's jay. Condor, 65:460-484.

----------. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bull., 81:293-329.

Buitron, D. 1983. Extra-pair courtship in black-billed magpies. Anim. Behav., 31:211-220.

Bumpus, H. [illegible]. The elimination of the unfit as illustrated by the introduced sparrow. Biol. Lect., Marine Biol. Lab., Woods Hole. pp.209-226.

Burckhardt, D. 1944. Mowenbeobachtungen in Basel. Ornithol. Beobacht., 5:49-76.

Caraco, T., S. Mortindale, and H.R. Pulliam. 1980. Avian flocking in the presence of a predator. Nature, 285:400-401.

Conder, P. 1949. Individual distance. Ibis, 91:649-655.

Craig, J.L., A.M. Stewart and J.L. Brown. 1982. Subordinates must wait. Z. Tierpsychol., 60:275-280.

Davis, D.E. 1959. Territorial rank in starlings. Anim. Behav., 7:214-221.

Dill, H.H., and W.H. Thornsbury. 1950. A cannon-projected net trap for capturing waterfowl. J. Wildl. Manage., 14:132-137.

Ealey, D.M. 1981. Determination of sex and the sex ratio in a population of American dippers in southeastern Alberta. Alberta Naturalist, Special Issue, 2:66-81.

Erpino, M.J. 1969. Age determintion of the black-billed magpie. Condor, 71:267.

Evans, L.T. 1936. A study of social hierarchy in the lizard (*Anolis carolinensis*). J. Genet. Psychol., 48:88-111.

Fungle, G.N., S.I. Rothstein, and C.W. Osenberg 1984. Signals of status in wintering white-crowned sparrows (*Zonotrichia leucophrys gambelli*). Anim. Behav., 32:86-93.

Fretwell, S.D. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). Bird-Banding, 40:1-25.

Gartlan, J.S. 1968. Structure and function in primate society. Folia Primat., 8:89-120.

Gauthreaux, S.A. 1978. The ecological significance of behavioral dominance. pp.17-54. *In*, Perspectives in Ethology. (P.P.G. Bateson, and P.H. Klopfer, eds.). Plenum, New York.

Geist, V. 1966. The evolutionary significance of mountain sheep horns. Evolution, 20:558-566.

Geist, V. 1971. Mountain Sheep. University Chicago Press. Illinois.

Goodwin, D. 1976. Crows of the World. Comstock, New York.

Green, P.T. 1980. Sexing rooks (*Corvus furgileus*) by discriminant analysis. Ibis. 124:320-325.

Harrington, B. 1973. Aggression in winter resident and spring migrant white-throated sparrows in Massachusetts. Bird-banding, 44:314-315.

Hediger, H. 1941. Wildtiere in Gefangenschaft. Butterworth, London.

Hepp, R.G., and J.D. Hair. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. Condor, 86:251-257.

Hinde, R.A. 1954. Changes in responsiveness to a constant stimulus. Brit. J. Anim. Behav., 2:41-55.

Humphrey, P.S., and K.C. Parkes. 1959. An approach to the study of moults and plumages. Auk, 76:1-31.

Johnson, J. 1972. Ecology of the black-billed magpie in southeastern Washington. M.Sc. Thesis, Washington State University, Pullman.

Johnston, R.F., D.M. Niles, and S.A. Rohwer. 1972. Hermon Bumpus and natural selection in the house sparrow (*Passer domesticus*). Evolution, 26:20-31.

Johnston, R., and R. Fleischer. 1981. Overwinter mortality and sexual size dimorphism in the house sparrow. Auk, 98:503-511.

Kaufmann, J.H. 1983. On the definitions and functions of dominance and territoriality. Biol. Rev., 58:1-20.

Ketterson, E.D. 1979. Aggressive behavior in wintering dark-eyed juncos: determinants of dominance and their possible relation to geographic variation in sex ratio.

Wilson Bull., 91:371-383.

Ketterson, E.D., and V. Nolan Jr. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analysis of winter populations. Auk, 99:243-259.

----------. 1983. The evolution of differential bird migration. *In*, Current Ornithology (R.F. Johnston, ed.). Plenum Press. New York.

Kikkawa, J. 1980. Winter survival in relation to dominance classes among silvereyes (*Zosterops lateralis chlorocephala*) of Heron Island, Great Barrier Reef. Ibis, 122:437-446.

Krebs, J.R., and N.B. Davies. 1979. Behavioural Ecology: An Evolutionary Approach. Oxford, Blackwell Scientific.

Lack, D. 1966. Population Studies of Birds. Oxford, Blackwell Scientific.

Lill, A. 1974. Sexual behaviour of the lek forming white-bearded manakin (*Manacus manacus trinitatis*). Z. Tierpsychol., 36:1-36.

Linsdale, J.M. 1937. The natural history of magpies. Pacific Coast Aviafauna. No. 25. Berkeley, California.

Lorenz, K. 1931. Bertrage zur Ethologie sozialen Corviden. J. Orn., 79:67-127.

----------. 1938. King Solomon's Ring. Methuen, London.

Lumia, A.R. 1972. The relationships among testosterone conditioned aggression, and dominance in male pigeons. Hormones and Behavior, 3:277-286.

Maier, R.A., and B.M. Maier. 1970. Comparative Animal Behavior. Wadsworth Publishing Company, Belmont, California.

Marascuilo, L.A., and M. McSweeney. 1977. Non-parametric and Distribtion-Free Methods for the Social Sciences. Brooks and Cole, California.

Marler, P. 1955-57. Studies of fighting in chaffinches. I-IV. Brit. J. Anim. Behav., 3:111-117, 3:137-146, 4:23-30, 5:29-37.

Maslow, A.H. 1940. Dominance quality and social behavior in infrahuman primates. Soc. Psychol., 11:313-324.

Morrison, A.S. 1976. Multivariate Statistical Methods, McGraw-Hill, New York.

Mugaas, J.N., and J.R. King. 1981. Annual variation of daily energy expenditure by the back-billed magpie: a study of thermal and behavioral energetics. Studies in Avian

Biology 5. Cooper Ornith., Soc.

Murphy, E.C. 1978. Breeding ecology of house sparrows: spatial variation. Condor, 80:180-193.

----------. 1980. Body size of the house sparrow: reproductive and survival correlates. Proc. Internat. Ornith. Cong., 17:1155-1161.

Murton, R.K., A.J. Isaacson and N.J. Westwood. 1966. The relationship between wood pigeon and their clover food supply and the mechanism of population control. J. Appl. Ecol., 3:55-96.

Noble, G.K., and M.Wurm. 1946. The effect of testosterone propionate on the black-crowned night heron. Endocrinology, 26:837-850.

O'Halloran, P.C. 1961. Dynamics of a reduced magpie population. M.Sc. Thesis. Montana State University. Missoula.

Patterson, I.J. 1977. Aggression and dominance in winter flocks of Shelducks (*Tadorna tadorna (L.)*. Anim. Behav., 25:447-459.

Powell, G.V.M. 1974. Experimental analysis of the social value of flocking by starlings (*Sternus vulgaris*) in relation to predation and foraging. Anim. Behav. 22:501-505.

Pulliam, H.R., and G.C. Millikan. 1982. Social organization in the non-reproductive season. *In,* Avian Biology. Vol. VI. (D.S. Farner, J.R. King, and K.C. Parkes, eds.). Academic Press, New York.

Reese, K.P., and J.A. Kadlec. 1982. Determining the sex of black-billed magpies by external measurements. J. Field Ornith., 53:417-418.

Rising, J. 1973. Age and seasonal variation in dimensions of House Sparrows (*Passer domesticus*), from a single population. *In,* Productivity, Population Dynamics, and Systematics of Granivorous Birds. (S.C. Kendeigh and J. Pinowski, eds.). Warsaw, Polish. Sci. Pub.

Rohwer, S. 1975. The social significance of avian winter plumage variability. Evolution, 29:593-610.

Rohwer, S., and P.W. Ewald. 1981. The cost of dominance and the disadvantage of subordination in a badge signaling system. Evolution, 35:441-454

Rowell, T.E. 1974. The concept of social dominance. Behavioral Biology, 11:131-154.

Salyer, J.C. 1955. Improvements in the cannon net traps. U.S. Fish and Wildl. Res., Wildl. Manag. Ser. No. 12. Washington, pg. 27 (multilith)

Schjelderup-Ebbe, V.T. 1922. Beitrage zur Sozialpsychologie des Haushulns. Z. Psychol., 88:225-252.

Scott, J.P., and E. Fredericson. 1951. The causes of fighting in mice and rats. Physiol. Zool., 24:273-309.

Searcy, W.A. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). Amer. Natur., 114:

Shields, W.M. 1977. The social significance of avian winter plumage variability: a comment. Evolution, 31:905-907.

Smith, J.N.M., R.D. Montgomerie, M.J. Taitt and Y. Yom-Tov. 1980. A winter feeding experiment on an island song-sparrow population. Oecologia, 47:164-170.

Sneath, P., and R.R. Sokal. 1973. Numerical Taxonomy. W.H. Freeman, San Francisco.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. W.H. Freeman, San Francisco.

Tatner, P. 1982. The density of breeding magpies (*Pica pica*) in an urban environment. Naturalist, 107:47-58.

Watson, A., and R. Moss. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. pp. 167-218. *In*, Animal Populations in Relation to Their Food Resources, (A. Watson, ed.). Blackwell Scientific Publishers, Oxford.

----------. 1971. Spacing as affected by territorial behavior, habitat and nutrition in red grouse (*Lagopus l. scoticus*). pp. 92-111. *In*, Behaviour and environment. The use of space by animals and men. (A.H. Esser, ed.). Plenum, New York.

Wiley, R.H. 1973. Territoriality and non-random mating in the sage grouse (*Centrocercus urophasionus*). Anim. Behav. Monogr., 6:87-169.

Wilson, E.O. 1975. Sociobiology: The New Synthesis. Belknap Press, Cambridge, Mass.

Wittenberger, J.F. 1981. Animal Social Behavior. Duxbury Press, Boston, Mass.

Yom-Tov, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone L.*). J. Anim. Ecol., 43:479-498.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall Inc., New Jersey.

IX. Appendix

Dominance Relationships Among Captive Black-billed Magpies

Appendix 1.

The number of agonistic interactions won and lost by the members of 17 groups of five black-billed magpies held under captive conditions. The birds are arranged in order of diminishing rank from left to right within each cage. Sex of birds in parentheses: M=male, F=female.

Cage 1

RM(M)	WG(F)	RG(F)	OG(F)	YG(F)
RM	4	0	0	0
WG		21	8	3
RG			4	25
OG				5
YG		3	2	

Cage 2

S(M)	GY(M)	BB(F)	GW(F)	BR(F)
S	7	7	33	40
GY		1	11	6
BB			3	6
GW				22

Cage 3

R(M)	S(M)	WR(M)	GR(M)	OR(M)
R	12	13	7	13
S		11	6	14
WR			3	18
GR		20		
OR			18	

Cage 4

RG(M)	GG(M)	RB(F)	WW(F)	BW(M)
RG	4	3	10	3
GG		6	9	2
RB			2	3
WW				9

Appendix 1. (continued)

Cage 5

	GG(M)	OY(M)	YW(M)	BR(F)	OR(F)
GG		4	0	9	6
OY			2	4	6
YW				3	3
BR					7

Cage 6

	O(M)	RW(F)	WB(F)	WO(F)	WW(M)
O		17	9	4	3
RW			27	7	11
WB				6	2
WO			5		2
WW			3		

Cage 7

	YS(M)	S(M)	OW(F)	YR(F)	BB(F)
YS		3	2	2	2
S			7	12	7
OW				6	3
YR					16

Cage 8

	BW(M)	Y(F)	GR(F)	RB(M)	BR(F)
BW		17	17	10	5
Y			13	9	0
GR				15	0
RB					2

Cage 9

	WB(M)	OY(F)	S(M)	WW(F)	WR(F)
WB		2	1	2	2
OY			14	19	17
S				6	3
WW					13

Cage 10

	BS(F)	RR(M)	GY(M)	RG(F)	S(F)
BS		11	10	12	8
RR			24	13	16
GY				6	15
RG					4

Appendix 1. (continued)

Cage 11

RY(M)	S(M)	OS(F)	BS(F)	WB(F)
RY	14	10	9	7
S		10	7	8
OS	1		3	2
BS				4

Cage 12

WS(M)	YG(F)	BR(F)	SO(F)	S(F)
WS	11	13	5	7
YG		11	13	7
BR	2		9	2
SO	1			14
S 2				

Cage 13

OR(M)	BY(M)	WO(M)	S(F)	SO(F)
OR	5	9	5	3
BY		17	19	0
WO			7	6
S				20
SO	5	2	1	

Cage 14

WR(M)	RY(M)	YG(M)	G(M)	SG(M)
WR	5	9	5	3
RY		17	9	0
YG			15	2
G				7

Cage 15

OO(M)	S(M)	OS(M)	Y(M)	SO(M)
OO	6	14	9	7
S		3	7	0
OS			5	0
Y		1		2

Cage 16

WW(M)	W(M)	GB(M)	GS(M)	YR(F)
WW	7	6	6	7
W		0	5	2
GB			2	0
GS			2	2

Appendix 1. (continued)

Cage 17

RS(F)	RR(F)	OO(F)	GS(F)	GG(F)
RS	11	5	7	10
RR		6	0	3
OO			8	1
GS		2	0	4

X. Appendix 2

Age and Sex Determination

of the Black-billed Magpie (*Pica pica*)

ABSTRACT

Past attempts at determining the age and sex of the black-billed magpie (*Pica pica*) have met with varying degrees of success. This paper shows that the length of the black tip of the 10th primary enables one to determine the age of individuals in a northern population of *Pica pica hudsonia* with 100% reliability. Measurements of wing chord and the depth of the bill at the nostrils correctly classified 95% of juveniles to the correct sex, whereas wing chord and the length of the bill at the commissural point correctly classified 98.7% of adult magpies according to sex. These criteria of sex, unlike those used by previous investigators, can be used throughout the year.

INTRODUCTION

It is often essential, when studying behavior of free-living birds to know the sex and age of the individuals involved. Such information is often difficult to acquire when the plumage of the species, in this case the black-billed magpie (*Pica pica hudsonia*), is not obviously sexually dimorphic . Although male magpies are generally larger than females (Linsdale 1937, Baeyens 1979, Mugaas and King 1981, Reese and Kadlec 1982), overlap in measurements makes it difficult to determine sex reliably. Some investigators have relied on reproductive behavior of previously marked birds to determine sex (Baeyens 1981). However, sex determination based on reproductive behavior is reliable only during the reproductive season and only for those birds which are reproductively active. The method developed by Reese and Kadlec (1982), based on discriminant function analysis of external measurements, is reliable only for part of the year (1 January to 25 March and from 20 April to 1 June). They used weight as a sex-discriminating variable, but during the egg-laying period the increased mass of females made weight an unreliable determinant.

Age is often difficult to assess, especially when the first pre-basic plumage is similar to the adult definitive basic plumage (Humphrey and Parkes 1959, Bancroft and Woolfenden 1982). The magpie completes the first pre-basic molt (partial) by late autumn, and retains its first pre-basic plumage for about a year. This plumage closely resembles the adult definitive basic plumage which is attained after its second pre-basic molt (complete). It is during this period, when magpies exhibit their first pre-basic plumage, that Linsdale (1937) and Erpino (1969) refer to them as juveniles; thereafter they are classified as adults (Linsdale 1937, Erpino 1969, Reese and Kadlec 1982).

Erpino (1969) used the shape of the reduced tenth primary (P10) and the length of the black tip of the fourth primary (P4) as subjective and objective criteria for age determination . Erpino (1969) further stated that the primaries of juvenile magpies had more black on their tips than did those of adults. However he failed to illustrate these differences, forcing the reader to make subjective decisions.

Discriminant function analysis (DFA) has been shown to be an effective method for determining which morphometric measurements are the best for classifying individuals according to sex and age (Green 1980, Ealey 1981). In this paper I use DFA to reveal which morphometric characteristics are useful in determining the sex and age of magpies throughout the year. I also illustrate part of the plumage criteria used by Erpino (1969) to determine age.

METHODS

A sample of 139 birds was collected in all seasons of 1981-1982 by the Divison of By-Law Enforcement, City of Edmonton, Alberta. It contained 98 juveniles and 41 adults. Eighteen morphometric measurements were taken on most (95%) birds (Table X-1). The age of all birds was based on the subjective methods of Linsdale (1937), Bent (1946), and Erpino (1969), and the technique checked against birds of known age. These data were analyzed by discriminant function analysis (DFA), using SPSS (Statistical Packages for the Social Sciences 1979). DFA selects from among the variables (measurements) those that best discriminate between the categories of sex and age. Often DFA selects more than one variable to discriminate between groups, thus increasing the reliability of the classification (Sokal and Rohlf 1981). Once known, the appropriate measurements can be used to determine the sex and age of unknown birds handled in the field.

RESULTS

A list of measurements taken and a description of them appear in Appendix 4. Accurate classification of the age of all birds can be achieved by using the measurement of the black tip of the 10th primary (TENDAR). This measurement was 100% accurate in classifying birds as juveniles or adults. A black tip of less than or equal to 11 mm classifies the individual as an adult and more than 11 mm as a juvenile (Figure X-1). Thus this measurement alone is all that is needed to determine age. The length of the black tip of P4 (FTHPRI) was not useful in determining age contrary to the suggestion of Erpino (1969); the amount of overlap between juveniles and adults made it unreliable. The shape of the white patches within the surrounding

Table X-1. Measurements (mm) of morphometric structures of both age and sex classes of black-billed magpies collected in the City of Edmonton, Alberta.

Character[a]	Juvenile				Adult			
	male n=60		female n=38		male n=27		female n=14	
	X	s.d.	X	s.d.	X	s.d.	X	s.d.
WINGCH	204.0	6.5	195.7	4.7	207.1	4.3	192.4	3.2
WINGBR	164.7	6.5	159.0	8.2	166.8	9.6	155.9	3.0
FTHPRI	24.5	3.1	22.8	2.5	19.6	4.0	20.6	5.1
TENDAR	20.5	5.3	21.8	3.9	7.7	2.0	8.4	2.0
TENLIT	36.1	6.0	34.4	5.5	43.6	6.7	41.8	5.7
LATREC	137.1	8.5	133.2	8.5	140.3	8.2	129.1	5.4
CENREC	260.2	24.2	253.9	12.6	293.4	14.1	260.4	21.8
LTBLCM	43.5	1.2	40.7	2.4	44.4	1.6	40.5	2.0
LTBLNS	26.5	1.1	25.4	3.9	26.3	1.6	23.6	1.6
DTBRIC	143.1	7.1	133.5	6.3	143.6	6.6	133.1	4.3
DTHNOS	135.8	5.5	125.5	5.4	135.8	6.7	125.4	3.7
WTHNOS	121.8	8.2	114.6	7.7	123.1	8.0	111.5	6.9
CULMEN	31.2	2.9	29.9	3.1	31.2	2.2	27.9	2.8
TARSUS	50.3	1.9	48.3	2.8	50.7	2.2	45.9	2.5
FOOT	77.1	2.5	74.2	2.8	77.4	3.3	72.0	3.4
HIDTOE	16.4	1.7	15.6	0.8	15.7	0.7	15.3	1.0
MIDTOE	24.3	1.9	23.2	1.6	23.8	2.2	22.6	1.9
WEIGHT	197.5	25.6	170.9	16.1	192.6	17.2	181.4	28.2

[a] Description of these structures given in Appendix 4.

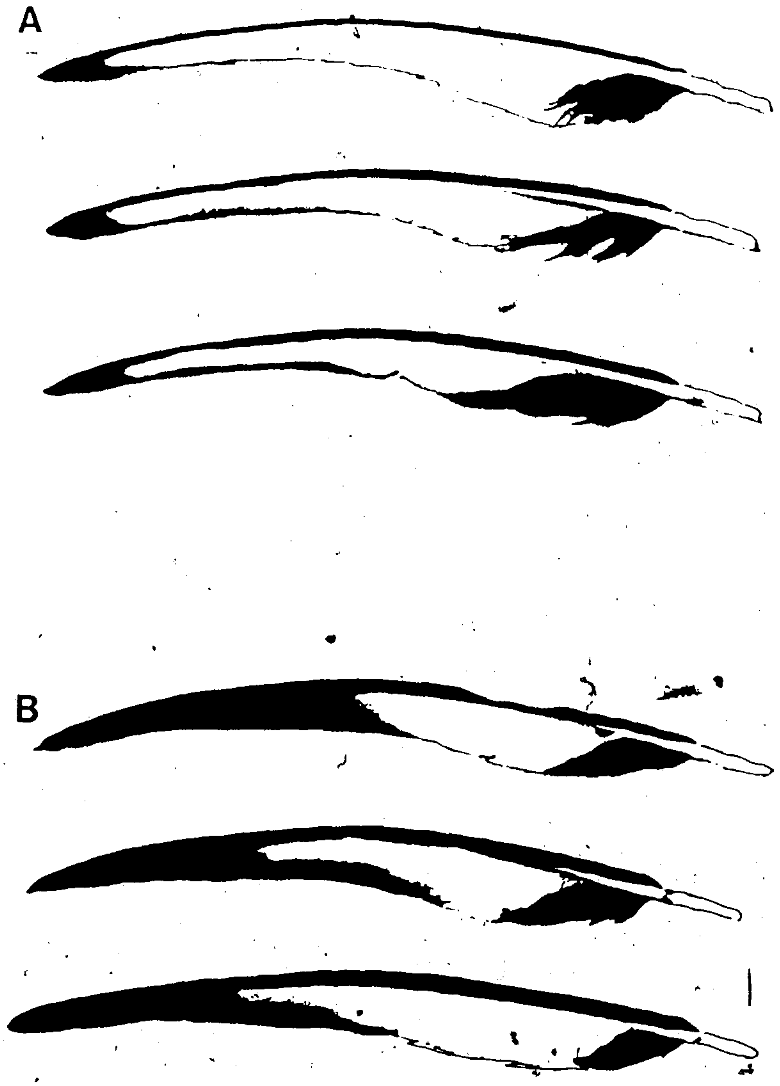

Figure X-1. Samples of the reduced tenth primary from the wings of adult (A) and juvenile (B) black-billed magpies collected in the City of Edmonton, Alberta.

black portion of the primaries of magpies can be used as a subjective criterion (Figure X-2). It is apparent that the primaries of juveniles have less well defined white areas than do those of adults. Adults have distinct edges to the borders of the white portion of their primaries, especially evident toward the distal tip of the feather. When used by an experienced investigator, this characteristic is reliable as an age-determining characteristic.

To discriminate between the sexes of juveniles, DFA selected wing chord (WINGCH) and depth of the bill at the mid-point of the nostril (DTHNOS) as being the most useful. These two measurements correctly classified the sex of 95% of juvenile birds in the sample. For adults, DFA selected WINGCH and length of bill from the commissural point (LTBLCM) as the best discriminators of sex. The discriminant function for these variables classified 98.7% of the adults in the sample correctly. A list of the critical measurements for both juveniles and adults appears in Tables X-2.

DISCUSSION

DFA was used to determine the appropriate morphometric measurements needed to classify magpies sampled in Edmonton, Alberta into the correct age and sex categories. Although the subjective criteria developed by Erpino (1969) to determine age were reliable, a measurement of the 10th primary (TENDAR) provided an objective means of determining age. The amount of black in the tip of P10 (TENDAR) was clearly the single best measurement for this purpose, especially for the naive investigator. DFA also provided appropriate criteria for use in the determination of sex of magpies throughout the year.

Geographic variation in morphology may not permit the use of critical values derived for this sample to be used for birds in other locations. This problem has arisen with other birds, for example dippers (*Cinclus mexicanus*) (Ealey 1981). Thus samples from other areas should be checked against the values for measurements presented in this paper.

Table X-2. The critical structures and their measurements for determining the sex of adult and juvenile black-billed magpies.

	length of bill from tip to commissural point		depth of the bill at the nostril	
	Adult		Juvenile	
wing chord [a]	male	female	male	female
190 (mm)	50[b]	49[c]	13.8[b]	13.7[c]
191	50	49	13.7	13.6
192	49	48	13.6	13.5
193	48	47	13.6	13.5
194	47	46	13.5	13.4
195	47	46	13.4	13.3
196	46	45	13.4	13.3
197	45	44	13.3	13.2
198	44	43	13.2	13.1
199	44	43	13.2	13.1
200	43	42	13.1	13.0
201	42	41	13.0	12.9
202	41	40	13.0	12.9
203	41	40	12.9	12.8
204	40	39	12.8	12.7
205	39	38	12.8	12.7
206	38	37	12.7	12.6
207	38	37	12.6	12.5
208	37	36	12.6	12.5
209	36	35	12.4	12.4
210	35	34	12.4	12.3

[a] For both adult and juvenile birds wing chord is used as a sex determining structure.

[b] Measurements are equal to or greater than the values given.

[c] Measurements are equal to or less than the values given.

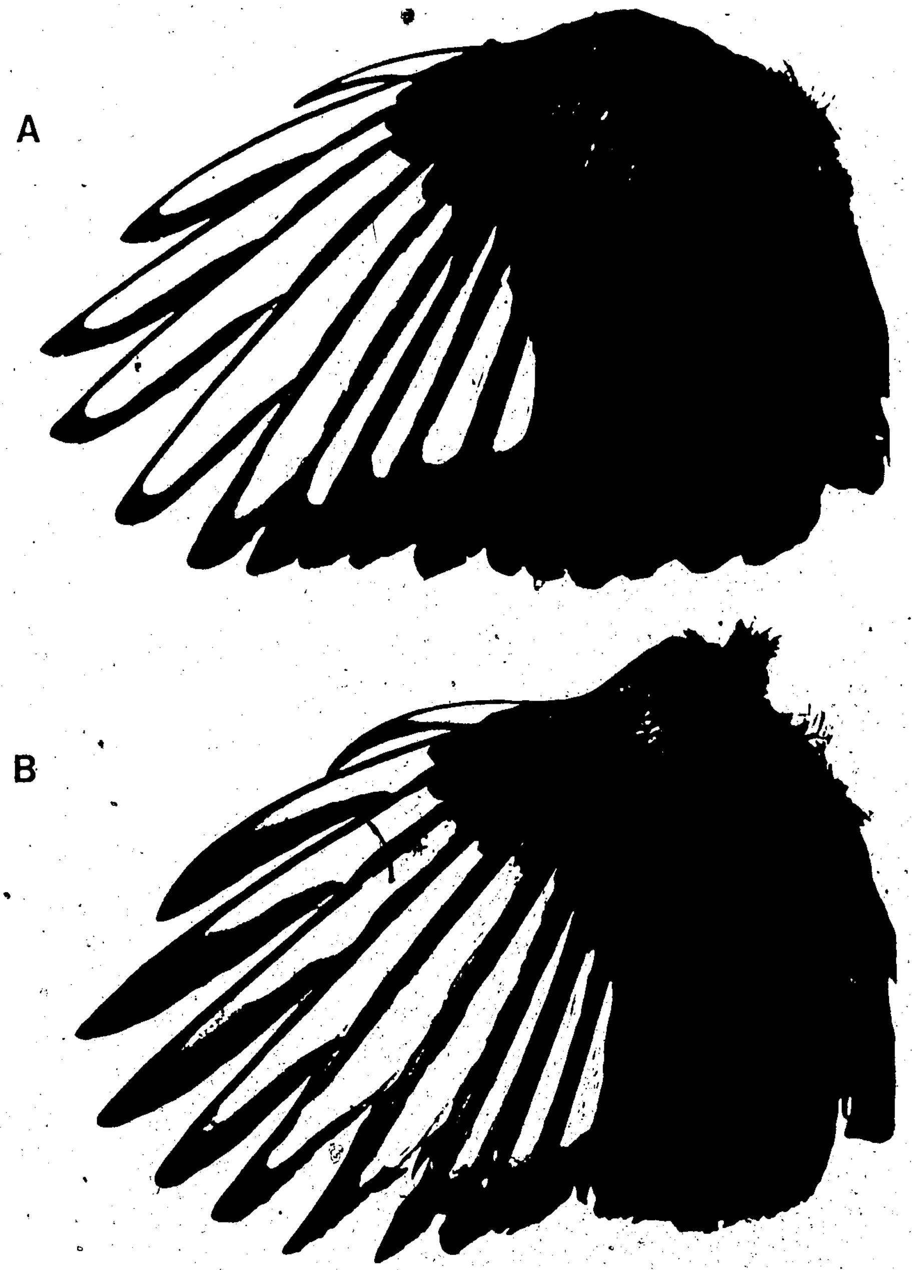

Figure X-2. The wing of an adult (A) and juvenile (B) black-billed magpie. According to Erpino (1969) the white within the primaries of a juvenile are less defined and more lancolate in shape than in adults.

XI. Appendix 3

A Technique for Trapping Territorial Magpies

ABSTRACT

A trapping technique used to capture territorial black-billed magpies (*Pica pica*) in an urban setting is described. Noose-covered wickets placed around a live decoy were effective in capturing at least one member of a pair of magpies in 93% of cases where it was tried. This technique appears superior to conventional methods for capturing magpies and may also be effective for capturing other territorial birds.

INTRODUCTION

As part of a behavioral study of black-billed magpies (*Pica pica*) conducted within the city of Edmonton, Alberta, it was necessary to capture and individually mark resident birds. However, their wary nature makes magpies difficult to capture. Conventional traps such as the ladder trap and the circular live trap (Alsager et. al. 1972) proved unsatisfactory because they were awkward to relocate, required prebaiting, and were difficult to maintain in an urban environment. Other traps such as the V-shaped drop trap (Johnson 1972), pheasant trap (Johnson 1972) , Bal-Chatri mat (Berger and Mueller 1959) and cannon nets (Dill and Thornsbury 1950, Salyer 1955) have met with limited success when used by other researchers (Buitron pers. comm., Reynolds pers. comm., Trost pers. comm.). Although Baeyens (1981) and Buitron (1983) captured magpies using monofilament-line leg snares placed around a live decoy bird or bait, they provided no clear description of these techniques. I describe here a similar trapping system using a tethered bird and noose-covered wickets.

METHODS

Noose-covered wickets (Figure XI-1) were made from 12-14 gauge (2 mm diameter) wire cut into approximately 32-cm lengths; sturdy wire clothes hangers can be used for this purpose. Each section was bent into a wicket with legs 10 cm long and a cross bar of 12 cm. Three or four slip nooses, 6 to 9 cm in diameter, were made from green nylon non-reflective fishing line (7.75-kg or 15-lb test) and attached to the cross bar. Hindsight suggests that the cross bar could be lengthened to hold more nooses.

The noose-covered wickets were pushed into the ground in a wagon-wheel configuration, leaving a circle of 40-cm diameter in the center in which to tether a live magpie decoy (Figure XI-2). Adult males seemed to elicit the best response when used as a decoy. Areas of short vegetation (rather than bare areas) were selected in order to camouflage the wickets and nooses. I found it important to stand the nooses at an angle oblique to the ground; usually this was accomplished by propping them against blades of grass. The decoy was fitted with a neck collar made from 18-kg

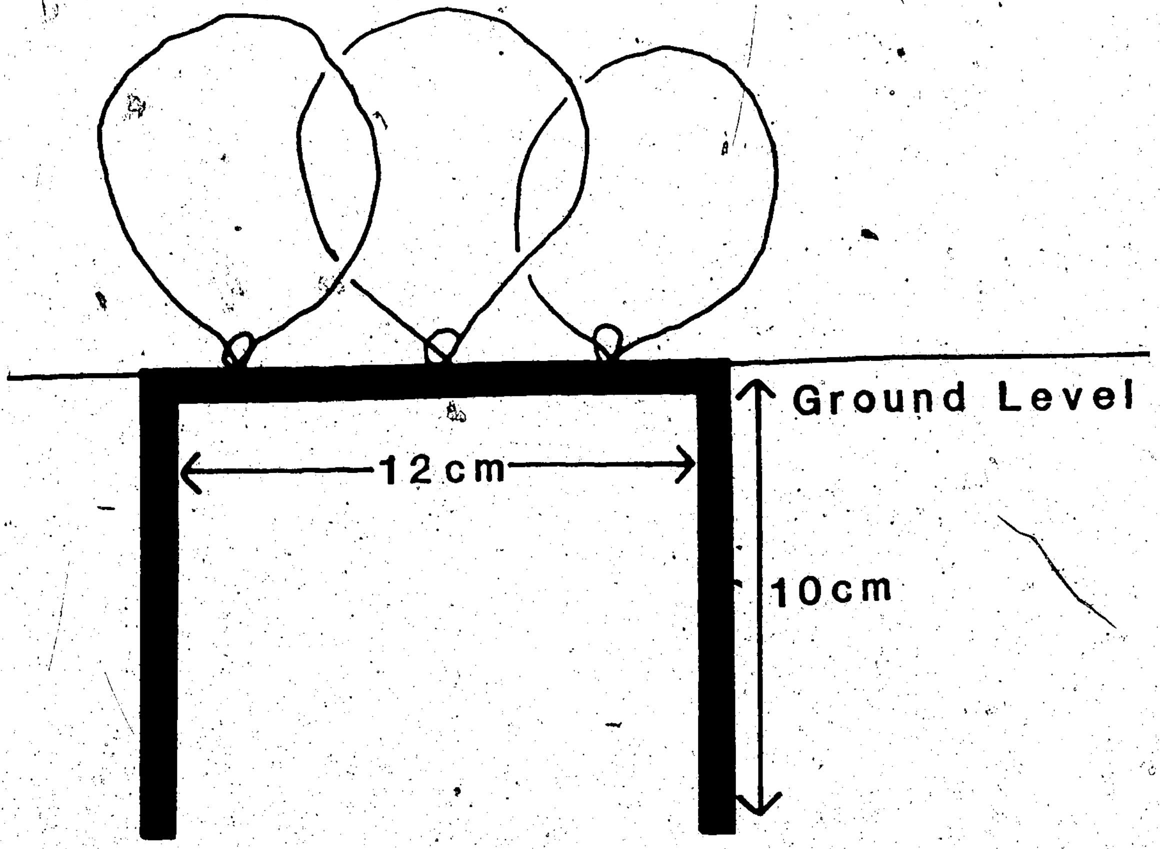

Figure XI-1. Nooses of monofilament non-reflective fishing line (7.75kg-15lb test), were attached to 12-14 gauge (2mm) wire bent in the shape of a square wicket. Wickets were placed flush with the ground. Nooses were propped up by vegetation (blades of grass).

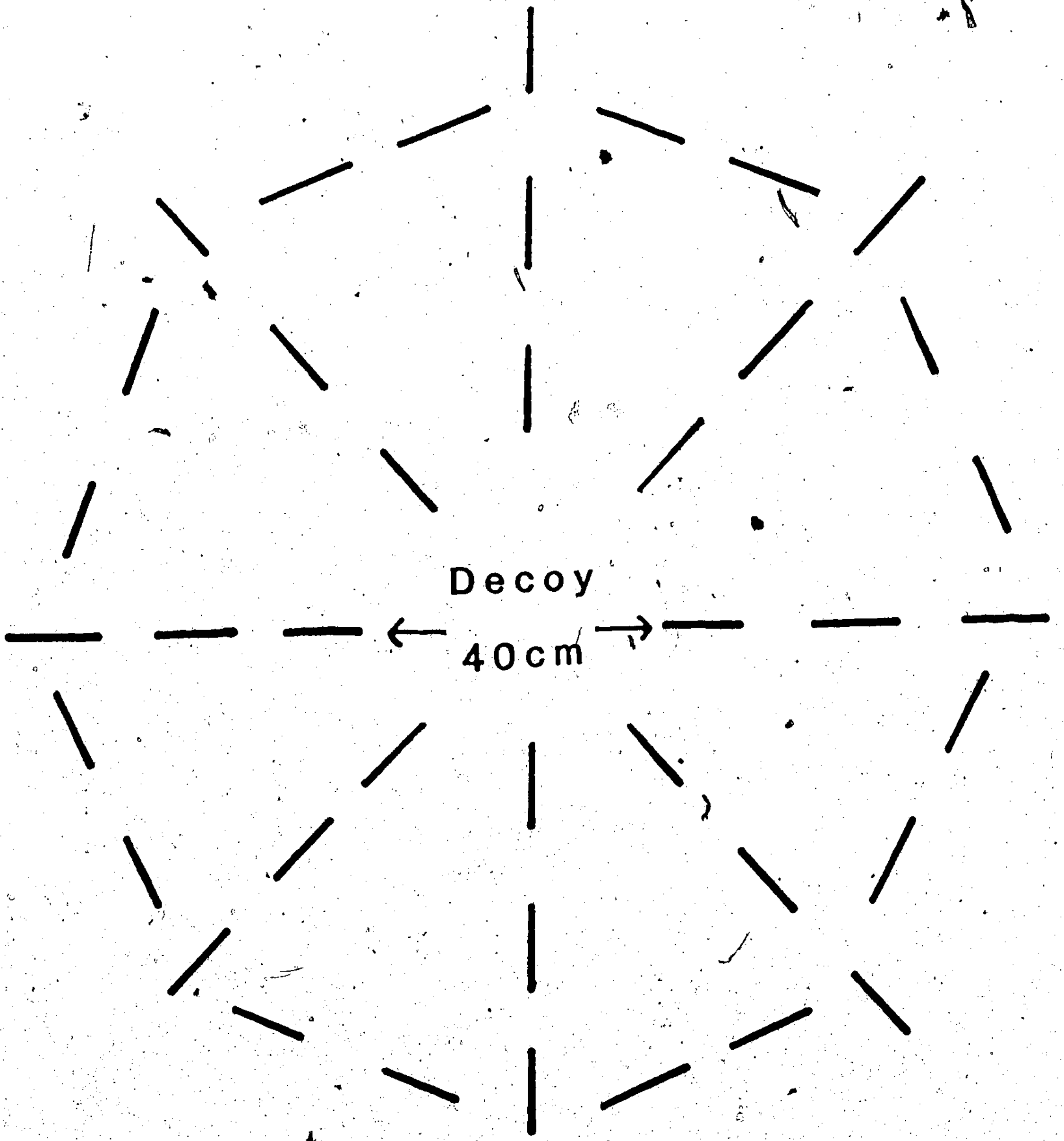

Figure XI-2. Wickets were placed in a wagon wheel configuration with the decoy bird placed at the center.

(40-lb) monofilament-line, large enough to move freely around the bird's neck but snug enough to not slip over its head. A 15.3-cm (6-inch) 18-kg (40-lbs) steel fishing leader with ball bearing swivels was used to tether the bird to the ground by clipping one end to the collar, and the other to a wicket placed at the center of the trap configuration.

By placing the trapping apparatus near the nest site during the reproductive season (March through July) the response time of the birds was decreased because of the intense activity near the nest at this time. Territorial owners often responded aggressively to the "intruding" bird and were caught within minutes. Captured birds struggled less if covered by a dark cloth while they were extracted from the leg snares.

RESULTS AND DISCUSSION

No territorial magpies were captured, during the breeding season in either ladder traps or circular traps, even when used for extended periods. Conversely, at least one bird was captured at 36 of 39 sites (93%) when noose-covered wickets were used. At 20 nest sites on the main study area, where trapping effort using this technique was greatest, both male and female were caught at 13, only one individual at 6, and neither at 1. No birds deserted their nests after being captured. Of 54 birds captured using nooses, 32 were males and 22 were females, based on measurements (Appendix 4) and behavior. Although not significant, this difference may indicate that males are more aggressive in defending territories or that males patrol their territories more often than females, which spend much time in their nests during the reproductive period.

Although it was not the intent of this study to recapture individuals, it is possible to do so using this technique. If an attempt at capturing a particular bird resulted in that bird escaping from the nooses, the technique is often more effective if tried again after a few days. The technique could be adapted for use on other birds which frequent the ground and exhibit strong territorial behaviour.

XII. Appendix 4

Description of Measurements

Appendix 4

Description of measurements used in this thesis. Abbreviations are in parentheses.

	Description of Measurement
wing chord	longest length from the bend of a closed wing to the longest primary (WINGCH)
wing breadth	longest length from the bend of a closed wing to the longest secondary (WINGBR)
P4	length of the black tip of the fourth primary measured from the distal tip of the white portion of the feather to the distal tip of the feather (FTHPRI)
P10 dark	length of the black tip of tenth primary measured from the distal tip of the white portion of the feather to the distal tip of the feather (TENDAR)
P10 light	length of the white portion of the tenth primary measured from the proximal (base) part of the feather vane to the distal portion of the white (TENLIT)
lateral rectrix	length of either of the most lateral rectrices from the point of insertion of the calamus to the distal tip of the rectrix (LATREC)
central rectrix	length of either of the most central rectrices measured from the point of insertion of the calamus to the distal tip of the rectrix (CENREC)

Appendix 4. (continued)

bill length 1	length of the bill measured from the commissural point to the distal tip of the upper mandible (LTBLCM)
bill length 2	length of the bill measured from the anterior edge of the nostril to the distal tip of the upper mandible (LTBLNS)
bill depth 1	depth of the bill measured at the base of the upper mandible adjacent to the bristles (DTBRIC)
bill depth 2	depth of the bill measured at the mid-point of the nostrils (DTBNOS)
bill width 1	width of the bill measured at the mid-point of the nostrils (WTBNOS)
culmen	length of the upper bill measured from the base of the upper mandible adjacent to the bristles to the distal tip of the upper mandible CULMEN)
tarsus	length of the tarsometatarsus (TARSUS)
foot	length of foot measured from the proximal end of tarsometatarsus to the distal tip of the pad of the third toe (FOOT)
toe 1	length of the hallux measured from the distal part of the pad to the proximal articulation of the toe (HIDTOE)
toe 2	length of the third toe measured from the distal tip of the pad to the proximal articulation of the toe (MIDTOE)
weight	measured in grams on a triple beam balance (model [illegible]00, Ohaus Scale Corporation) (WEIGHT)