National Library of Canada
Canadian Theses Service
Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Service des thèses canadiennes

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis su[illegible]r microfilming. Every effort has been made to en[illegible]ighest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, tests publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

NL-339 (r. 88/04)

Canada

THE UNIVERSITY OF ALBERTA

DISPERSAL, DOMINANCE BEHAVIOUR, AND BODY RESERVES IN MALLARDS DURING WINTER: MECHANISMS INVOLVED AND IMPLICATIONS FOR THE INDIVIDUAL

by

RICHARD PATTENDEN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL
FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
SPRING 1988

ISBN 0-315-42744-2

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: Richard Keith Pattenden

TITLE OF THESIS: Dispersal, Dominance Behaviour, and Body Reserves in Mallards during Winter: Mechanisms Involved and Implications for the Individual

DEGREE FOR WHICH THESIS WAS PRESENTED: Master of Science

YEAR THIS THESIS GRANTED: 1988

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(Signed) Richard Pattenden

PERMANENT ADDRESS:

52 - 12 avenue
Deux Montagnes, Quebec
J7R 3S2

Date November 17, 1987

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate studies and Research, for acceptance, a thesis entitled DISPERSAL, DOMINANCE BEHAVIOUR, AND BODY RESERVES IN MALLARDS DURING WINTER: MECHANISMS INVOLVED AND IMPLICATIONS FOR THE INDIVIDUAL submitted by RICHARD PATTENDEN in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

....

Supervisor

....

....

Jan O. Murie ....

....

Date ..... Nov 17/87 .....

Abstract

Reasons for a biased sex ratio in isolated populations of wild mallards (*Anas platyrhynchos*) wintering at a northern latitude (53° 35'N), were investigated. As well, dominance behaviour and effects of body reserves on the well being of the individual and its subsequent reproductive performance were examined using a flock of captive yearling mallards.

A sex ratio biased towards males existed at the onset of winter during both years of study, but during one environmentally harsh winter the proportion of females in the population, as well as the size of the latter, continued to decline over winter. Differential dispersal at the onset of winter was probably the major factor creating biased sex ratios in most northern wintering duck populations, a bias that apparently can be exacerbated by adverse enviromental conditions.

Among captive mallards, males dominated females and paired birds dominated singles. Dominance status of an individual, established during early life, was not related to dominance status as an adult. Of several correlates measured within each sex only hatch date was related to dominance status. Little overt aggression was observed during the study. Behavioural, rather than physical, cues probably mediated through hormone levels, were used to establish dominance relationships. The level of resource limitation (food, loafing space) affected interaction rates, supporting the idea that interactions observed among wild ducks represent competition for limited resources. Dominant individuals acquired preferred loafing locations more often and paired earlier than subordinates suggesting there is an advantage to being dominant. However, dominance status did not influence the level of lipid reserves acquired during competition for limited food resources, nor success in pairing.

Low body weight, an indication of reduced body reserves, delayed initiation of courtship and pairing, and decreased the number of permanent pair bonds formed. However, pairing date was not correlated with laying date. Low body weight during the winter period had a greater influence on laying date than low body weight during spring but neither affected clutch size. This suggests that an individual arriving on the breeding grounds with low body reserves relative to others,will have a lower reproductive output that year.

Acknowledgements

This research was funded by a grant from the North American Wildlife Foundation through the Delta Waterfowl and Wetlands Research Station and by grants to D.A. Boag and myself from the National Sciences and Engineering Research Council of Canada (NSERC). The Brooks Wildlife Center of the Alberta Fish and Wildlife Division provided facilities for the hatching, maintenance and breeding of the birds. I thank Gary Ash and R.L. & L. Environmental Services Ltd. for providing access to their Xerox 6085 Word Processor and Laser Printer free of charge.

I thank my supervisor, Dr. D.A. Boag who provided advice, guidance and editorial assistance throughout the course of this study. I am indebted to the personnel at the Brooks Wildlife Center who gave me assistance whenever it was needed, especially J. Archer, L. Ripley, B. Beasley, R. Antil and R. Schuler. I acknowledge the help given to me by my assistants R. Chubylo and B. Lepizki.

Special and sincere thanks go to my wife Chantal, who endured my absence during the field work, who gave me moral support whenever it was needed, and who provided invaluable typing expertise during the prolonged write-up stage of this thesis.

Table of Contents

Chapter Page

Chap[redacted] Page

List of Tables

List of Figures

I. INTRODUCTION

In the past 30 years much information has been published on the ecology and management of North American waterfowl (Anatidae). Despite this voluminous literature there is still relatively little known about the ecology of waterfowl during the winter period (Reinecke 1981, Anderson and Batt 1983). Recent studies have documented the existence in winter of a differential distribution of the sexes (Alexander 1983), dominant-subordinate relationships (Paulus 1983), and inter-seasonal influences on recruitment rates of ducks (Heitmeyer and Fredrickson 1981), yet the mechanisms producing each of these phenomena are not understood.

In many species of waterfowl females migrate farther south than males (Lebret 1950, Nichols and Haramis 1980, Nilsson 1983). Two hypotheses are used to explain this phenomenon: 1) differences between the sexes in body size create differences in the ability to fast and store body reserves (Calder 1974), such that larger males survive better farther north than smaller females, and 2) competition between the sexes occurs in which dominant males force subordinate females to move away (farther south) (Gauthreaux 1978). As yet, the relevance of either hypothesis to waterfowl, however, has not been clarified.

Several authors have observed that some individuals (males) are dominant to others (females) and suggest that subordinates incur the cost of exclusion from critical resources (Hepp and Hair 1984, Alexander 1987). Yet the criteria used to decide dominance status and the effects of exclusion on the individual, are not well understood.

Analysis of empirical data gathered over many years showed that environmental conditions on the wintering grounds were correlated with recruitment rates the following year (Heitmeyer and Fredrickson 1981, Kaminiski and Gluesing 1987). It is possible that delayed pairing (Brodsky and Weatherhead 1985), and/or a reduction in body reserves (Heitmeyer 1985) during the winter period, may be responsible for this decrease in reproductive output but few studies have addressed this question experimentally.

In this thesis, I present the results of a study investigating changes in sex ratio in a population of wild mallards (*Anas platyrhynchos*) wintering on the North Saskatchewan River within the City of Edmonton, Alberta. A subsequent study examined mechanisms of dominance behaviour in mallards, the consequences of this behaviour, and how variable body reserves influenced individuals in a captive flock of mallards. This species was selected because: 1) a population, existing at the northern edge of its winter range (Bellrose 1976), was readily accessible, 2) it is easily raised and observed in captivity, and 3) it is one of the few species for which a good body of published literature on its winter ecology exits.

I present the results in three chapters. The first (Chapter II) deals with the timing and causes of female disappearance in a population of wild mallards. The second (Chapter III) addresses the questions: is dominance behaviour prevalent in flocks of captive mallards? how is it manifested? and does it affect the well-being of the individual? The third (Chapter IV) reports on the relationship between body reserves and courtship activity, pairing, and reproduction. Chapter V integrates these results and discusses the importance of dominance status and body reserves during the winter period on the well being of the individual.

LITERATURE CITED

Alexander, W.C. 1983. Differential distributions of wintering diving ducks (*Aythyini*) in North America. Am. Birds 37: 26-29.

Alexander, W.C. 1987. Aggressive behavior of wintering diving ducks (*Aythyini*). Wilson Bull. 99: 38-49.

Anderson, M. G., and B.D. Batt. 1983. Workshop on the ecology of wintering waterfowl. Wildl. Soc. Bull. 11:22-24.

Bellrose, F.C. 1976. Ducks, Geese and Swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Brodsky, L.M., and P.J. Weatherhead. 1985. Time and energy constraints on courtship in wintering American black ducks. Condor 87: 33-36.

Calder, W.A. 1974. Consequences of body size for avian energetics. Pp. 86-144 *in* Avian Energetics (R.A. Paynter, Ed.). Nuttall Ornithol. Club Publ. No. 15, Cambridge, Massachusetts.

Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. Pp. 17-54 *in* Perspectives in Ethology, Vol. 3 (P.P.G. Bateson, and P.H. Klopfer, Eds.). Plenum Press, New York, New York.

Heitmeyer, M.E. 1985. Wintering strategies of female mallards related to dynamics of lowland hardwood wetlands in the upper Mississippi delta. Unpubl. Ph. D. dissert., University of Missouri, Columbia, Missouri.

Heitmeyer, M.E., and L.H. Fredrickson. 1981. Do wetland conditions in the Mississippi delta hardwoods influence mallard recruitment? Trans. North Am. Wildl. Nat. Resour. Conf. 46: 44-57.

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

Kaminski, R.M., and E.A. Gluesing. 1987. Density and habitat related recruitment in mallards. J. Wildl. Manage. 51: 141-148.

Lebret, T. 1950. The sex ratios and the proportion of adult drakes of teal, pintail, shoveler, and wigeon in the Netherlands, based on field counts made during autumn, winter and spring. Ardea 38: 1-18.

Nichols, J.D., and G.M. Haramis. 1980. Sex-specific differences in winter distribution patterns in canvasbacks. Condor 82: 406-416.

Nilsson, L. 1983. September and January counts as a measure of changes in south Swedish mallard populations. Wildfowl 34: 89-98.

Paulus, S.L. 1983. Dominance relationships, resource use, and pairing chronology of gadwalls in winter. Auk 100: 947-952.

Reinecke, K. J. 1981. Winter waterfowl research needs and efforts in the Mississippi Delta. Int. Waterfowl Symp. 4:231-236.

II. SKEWED SEX RATIO IN A NORTHERN WINTERING POPULATION OF MALLARDS

INTRODUCTION

In several migratory bird species inhabiting north temperate regions, females tend to be distributed farther south than males during the winter period. This phenomenon has been observed for puddle ducks (Anatini) (Lebret 1950, Sugden et al. 1974, Nilsson 1983, Perdeck and Clason 1983, Hepp and Hair 1984, Jorde et al. 1984), bay ducks (Aythyini) (Nichols and Haramis 1980, Alexander 1983), sea ducks (Mergini) (Anderson and Timkin 1972, Sayler and Afton 1981), as well as other bird species (King et al. 1965, Ketterson and Nolan 1976, Myers 1981, Dolbeer 1982, Smith and Nilsson 1987). Three hypotheses have been proposed to account for this difference in migratory tendency between the sexes.

The "arrival time hypothesis" states that if intrasexual selection confers a reproductive advantage to individuals (males) which arrive first on the breeding grounds (e.g. for territory establishment and mate acquisition), then males should winter as close as possible to the breeding grounds (Ketterson and Nolan 1976, Myers 1981). Among waterfowl, however, most species pair before arrival on the breeding grounds and before territory establishment (Bellrose 1976). Thus no selective advantage would accrue to these species in having males winter as far north as possible.

According to the "body-size hypothesis", greater cold tolerance and fasting ability, reflected in body size (Calder 1974), allow the larger sex to winter in more northern and rigorous climates (Ketterson and Nolan 1976, Ketterson and King 1977). Among ducks, males tend to be larger than females (Bellrose 1976), and wild populations of waterfowl that winter in northern areas generally lose weight and are in their poorest physical condition during periods of cold stress (Prince 1979, Reinecke et al. 1982, Whyte and Bolen

1984). There is also evidence suggesting that females are more sensitive to cold (Smith and Prince 1973, Bennet and Bolen 1978, Whyte and Bolen 1984), but sex specific mortality during harsh winter weather has not been observed (Roseberry 1962, Boyd 1964, Bennet and Bolen 1978).

Finally, the "dominance hypothesis" states that intersexual competition for limited resources leads the subordinate sex to migrate beyond the winter distribution of the dominant sex (Gauthreaux 1978, Ketterson and Nolan 1979). In many duck species males dominate females (Nichols and Haramis 1980, Hepp and Hair 1984, Heitmeyer 1985) and competition between the sexes has been implicated for what are assumed to be limited resources (Sayler and Afton 1981, Paulus 1983, Hepp and Hair 1984, Alexander 1987).

It is unclear, however, which of these hypotheses best explains the proximate mechanism for differential distribution reported for the sexes during the winter period. If competition for limited resources were the major cause of dispersal, one would predict that females should disperse from a local population at the onset of the limitation of the resources (i.e. the beginning of winter). By contrast, one would predict a gradual change in the sex ratio to occur throughout the winter period if selective mortality were responsible. These predictions can be compared with observed changes recorded in the sex ratio of populations of ducks wintering at the northern edge of their winter range.

The mallard (*Anas platyrhynchos*) is a holarctic species that winters farther north than any other puddle duck (Bellrose 1976) and exhibits a sex ratio heavily biased towards males in northern parts of its winter range (Sugden et al. 1974, Jorde et al. 1984). The object of this study was to document the chronology and rate of female disappearance in an isolated population of mallards wintering north of their normal winter range (Bellrose 1976).

STUDY AREA AND METHODS

The population studied winters on the North Saskatchewan River within the City of Edmonton, Alberta (53° 35' N, 114° 30' W). Effluent from a sewage treatment facility (major food source) and an electrical power generating station maintains approximately 2-4 km of open water (20-75m wide) during the winter period (November to March). Waste grain in surrounding agricultural fields is used by the mallards as a food source during periods of minimal snow cover.

The ducks were counted on a weekly basis (weather permitting) during the winters of 1984-85 and 1985-86. From observation points overlooking major roost sites I used a Bushnell spotting scope (15X40) to count individuals in the population and determine their sex. Each recorded count and sex ratio was treated as an individual data point. Those days on which < 100 individuals were counted (1984/85:5,1985/86:2) were omitted from the analysis to reduce the incidence of potentially inaccurate estimates of proportions (Sokal and Rohlf 1981). The data sets were subjected to linear regression analyses using the BMDP computer package (Dixon et al. 1983). Proportions were arcsine transformed. Simple G-tests and G-tests of independence with William's correction, and t-tests were used according to Sokal and Rohlf (1981). Weather information was obtained from the Atmospheric Environment Service, Environment Canada, at the Edmonton Municipal Airport. Because the nearest major wintering population is 300 km south I assumed that no immigration into my study population occurred after freeze-up (mid to late November).

RESULTS

The winter of 1984-85 was colder on average, had more days below -20° C and had greater snow depth than 1985-86 (Table II-1). An exception to this generalization was the month of November which was warmer in 1984 than 1985 (-8.5°C ± 4.7 vs -

Table II-1: Weather conditions within the city of Edmonton for the winters (November 1 - March 20) [illegible] and 1985/86

Year	Daily temperature(C°) $\overline{X} \pm SD$	Daily snow depth(cm) $\overline{X} \pm SD$	Number of days with daily temperature < -20°C
1984/85	-9.6 ± 9.3	21.9 ± 7.9	28
1985/86	-6.6 ± 9.3	6.9 ± 4.4	14
Difference	$P < 0.01$[1]	$P < 0.001$[1]	$P < 0.05$[2]

1 Based on t-test (two-tailed probability).
2 Based on simple G-test.

$12.9°C \pm 10.0; t = 2.171, df = 29, P < 0.05$). For this reason freeze-up of the river was later in 1984 (between November 20-25) than in 1985 (November 15-20).

Population counts were variable in both years (Figs. II-1, and II-2), but general trends were apparent. In 1984-85, there was a significant ($P < 0.01$) and relatively constant decline from early December (≈ 500 birds) to mid-March (≈ 350 birds). During 1985-86 a different trend was apparent. Having removed from the analysis the data points recorded before and during freeze-up of the river (Nov1-Nov20, 1985), when changes in population size probably reflected the movement of migrating flocks through the area, I determined that the decline in numbers of mallards observed between early December and mid-March was not significant ($P > 0.50$), and that the population remained at around 420 individuals.

The proportion of females in the population declined significantly during and just after freeze-up in both years of the study (Figs. II-3, and II-4). In 1984/85, the observed proportion went from 50 to 37% (G-test; $P < 0.005$), within a 11-day period (Nov. 27-Dec. 7); in 1985/86 it dropped from 56 to 37% (Linear regression; $P < 0.01$) in 32 days (Nov. 1-Dec. 2). In each year the proportion of females in the population in early December was the same ($P > 0.10$), but trends observed for the remainder of the winter were not similar. In 1984-85 the proportion of females declined significantly between mid-December and March from 37 to 32% ($P < 0.01$); whereas in 1985-86 the proportion remained stable at 37% ($P > 0.50$).

DISCUSSION

It appears that differential movement of the two sexes, with relatively more females than males emigrating at the onset of winter, was the main reason for a skewed sex ratio in these populations of mallards. In both winters an initial rapid decline was observed in the proportion of females. Dispersal in response to the onset of adverse weather conditions has been observed in several duck species (Bennet and Bolen 1978, Sayler and Afton 1981,

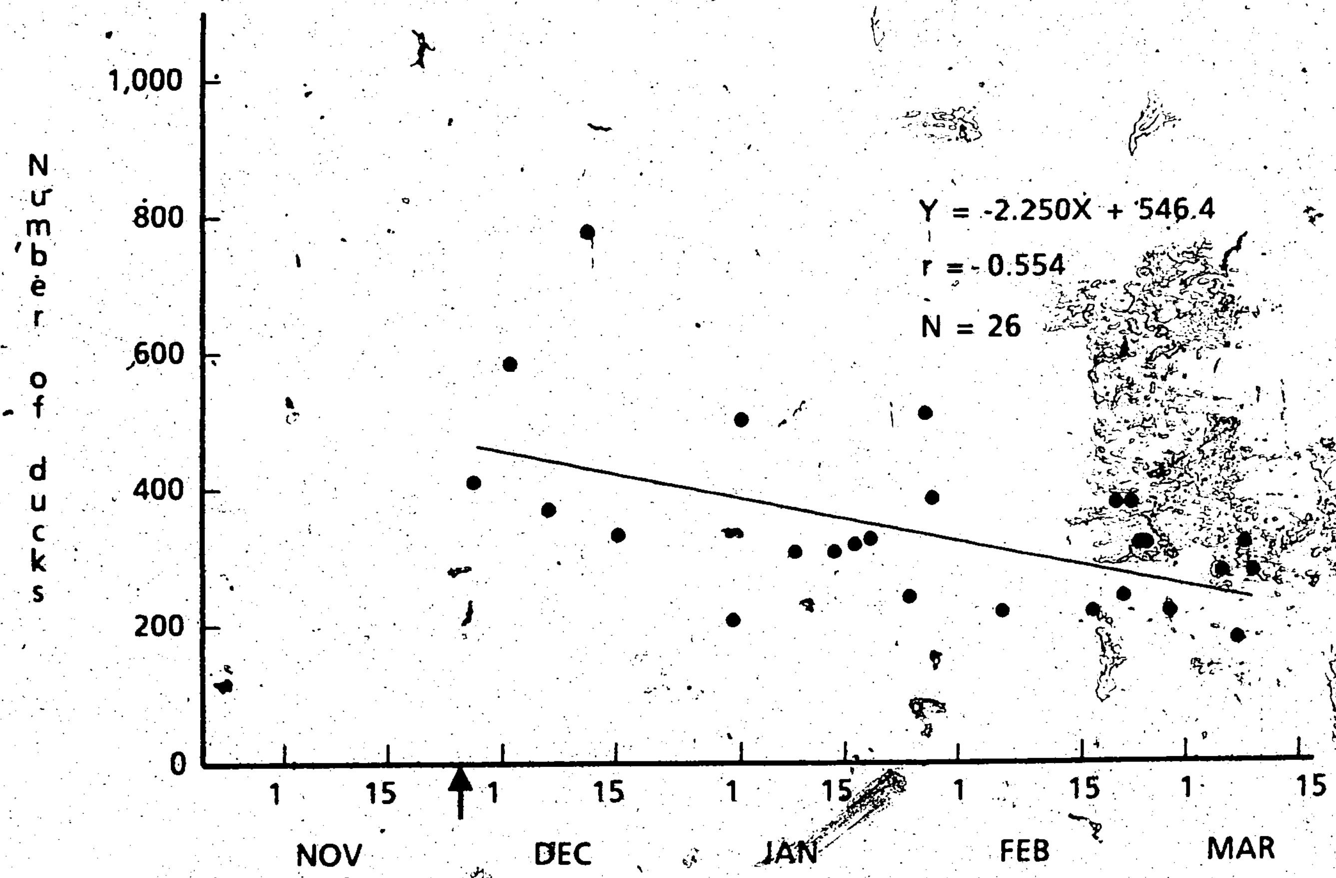


Figure II-1: Relationship between number of mallards counted and date during the winter of 1984/85. Arrow represents date of river freeze-up.

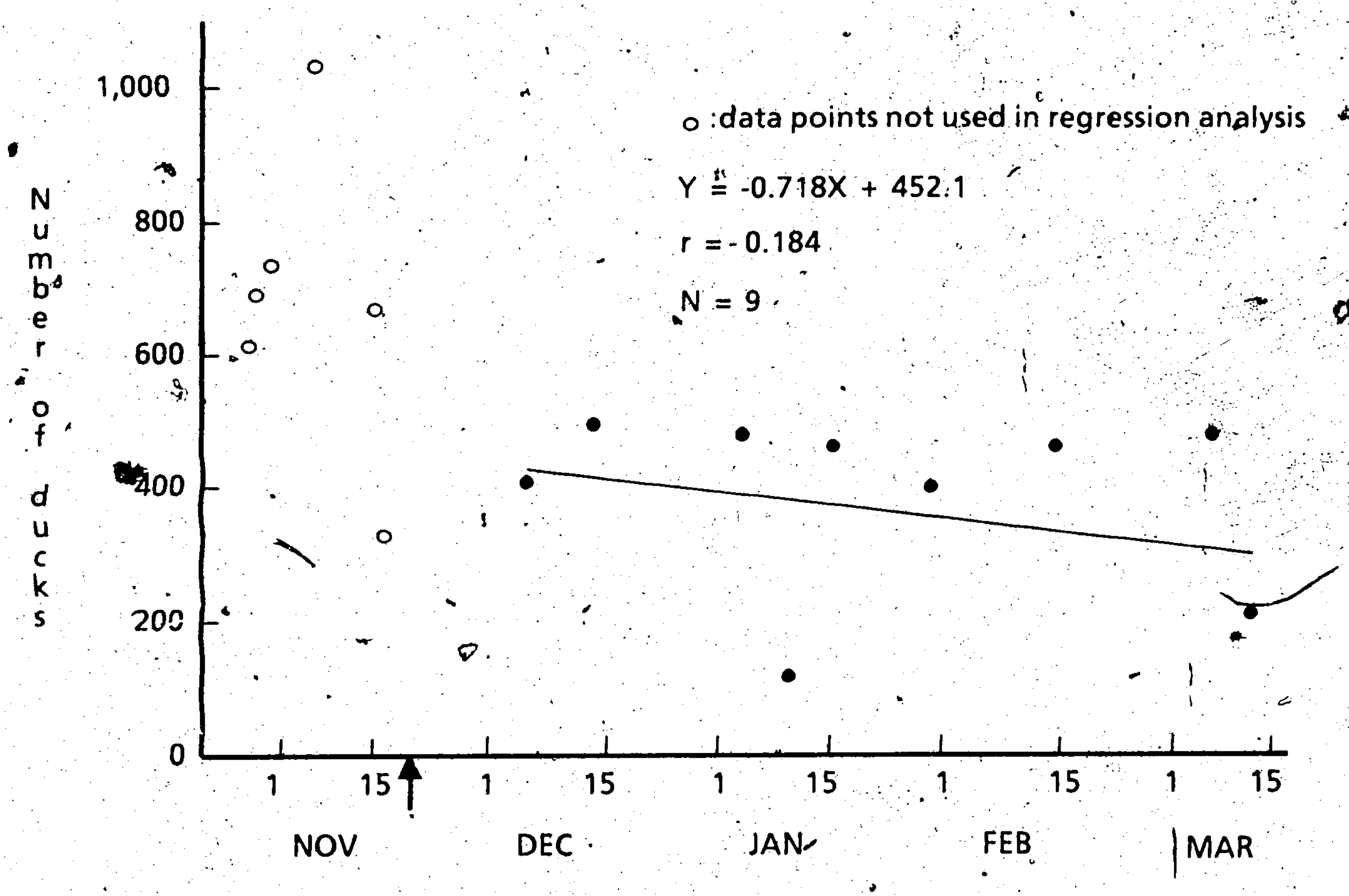


Figure II-2: Relationship between number of mallards counted and date during the winter of 1985/86. Arrow represents date of river freeze-up.

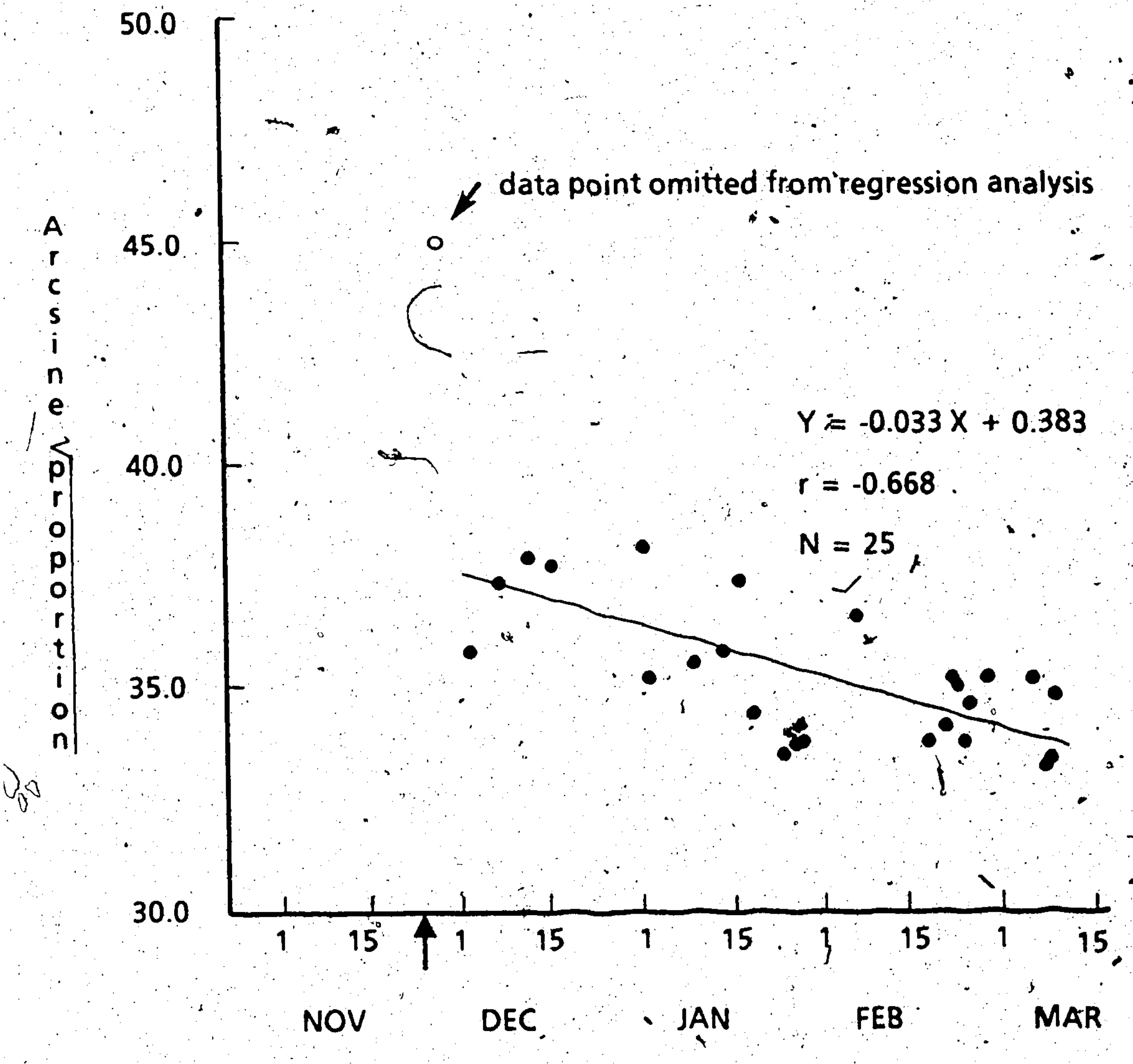


Figure II-3: Proportion of population (population = 500-350 birds) composed of female mallards during winter of 1984/85. Arrow represents date of river freeze-up.

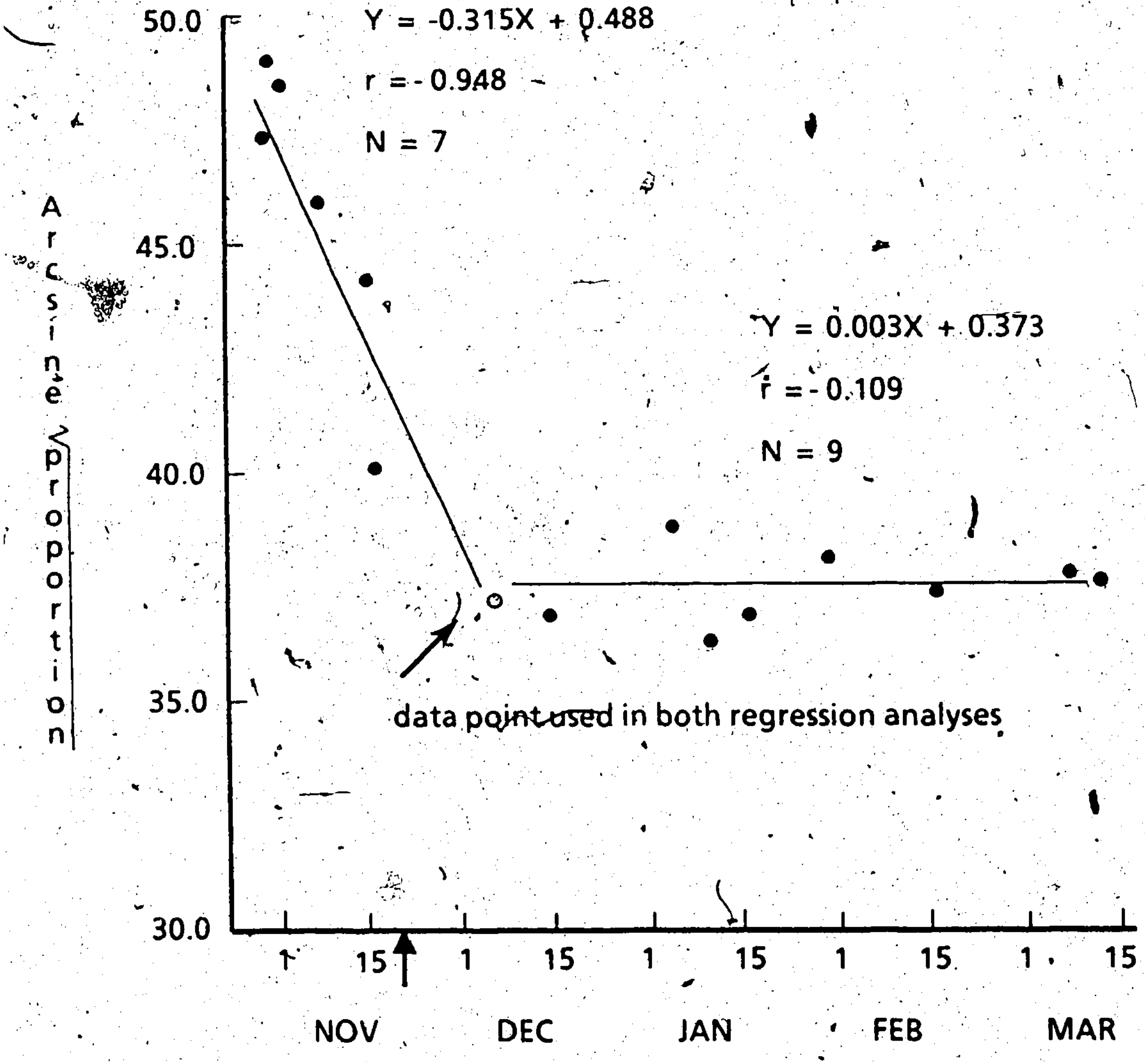


Figure II-4: Proportion of population (population ≈ 420 birds) composed of female mallards during winter of 1985/86. Arrow represents date of river freeze-up.

Nilsson 1983, Heitmeyer 1985). Bellrose and Crampton (1970) suggested that the winter distribution patterns of ducks (i.e. population size, sex and age ratios) were influenced by weather factors such as temperature, ice and snow conditions. Nilsson (1983, 1984), Perdeck and Classon (1983), and Nichols et al. (1983) found that regional and yearly distribution patterns of ducks were related to the severity of climatic conditions on the wintering grounds. Evidence from this study and others supports the suggestion made by Ketterson and Nolan (1979) that the sex ratio in wintering populations is established via differential emigration before sex specific mortality can influence the population composition, but the reason for differential emigration is unclear.

The onset of the winter period in north temperate regions is often characterized by rapidly falling temperatures and a sudden decline in available food (Fretwell 1972). This creates two immediate problems with which waterfowl must cope: 1) reduction in available space (through ice formation on waterbodies) and food, both terrestrial (waste grain) and aquatic, promoting intraspecific competition (Gauthreaux 1978), and 2) falling temperatures which increase energy demands (Calder 1974). Dispersal to less stressful environments assumed to exist farther south would be a means of escaping both problems.

Interactions between dominant males and subordinate females for food and loafing areas have been documented for several duck species (Nichols and Haramis 1980, Paulus 1983, Hepp and Hair 1984, Heitmeyer 1985, Alexander 1987), and it has been suggested that this competition may force females to disperse to more southern areas (Sayler and Afton 1981, Alexander 1983, 1987, Hepp and Hair 1984). Nichols et al. (1983) suggested that a threshold prompting this dispersal is reached at 0° C (i.e. ice cover versus no ice). Also populations that have ready access to artificial food sources show little tendency to disperse (Sugden et al. 1974, Nilsson 1976). This suggests that competition for food and/or space, rather than thermoregulatory costs, causes differential emigration in mallards.

In contrast to the rapid decline observed in both years at the onset of winter, the proportion of females in the population (as did population size) declined slowly in 1984-85, but not in 1985-86. Since midwinter dispersal is unlikely in this population (nearest major wintering population is 300 km south) the decline was probably due to mortality. During 1984-85 there were three potential sources of mortality for this population: shooting to control crop depredation, fouling of plumage by waste oils causing loss of thermoregulatory ability, and death through starvation and/or exposure to extreme cold. A combination of all three probably reduced the overall population size, but only the last mortality factor was likely to be sex biased in this local population, affecting females more than males.

Mortality attributed to severe weather has been reported in several populations of wintering ducks (Roseberry 1962, Boyd 1964, Nelson 1978). Sugden et al. (1974), who studied a wintering population of mallards in southern Alberta, noted a low but continuous mortality rate throughout the winter, apparently through starvation. During periods of extreme cold, waterfowl appear to be stressed and modify their behaviour to reduce heat loss (Brodsky and Weatherhead 1984, Jorde et al. 1984). In this study, such behaviour (i.e. continuous resting, huddling) were observed and several dead emaciated birds (4 females, 3 males) were found during periods of extreme cold in 1984-85. The winter period of 1984-85 was more severe than 1985-86 with low temperatures being reached on numerous occasions (Table II-I). Indirect evidence (a continual decline in the proportion of females in the population), suggests that females were probably suffering higher mortality rates than males.

If the harsher winter of 1984-85 caused the apparent differential mortality of females, the physiological limitation hypothesis, proposed by Ketterson and Nolan (1976), is supported. Females of several waterfowl species may be more sensitive to extreme cold, than males (Smith and Prince 1973, Ketterson and King 1977, Bennet and Bolen 1978, Whyte and Bolen 1984) but there is no direct evidence supporting sex specific mortality caused by physiological limitations in waterfowl. An alternative explanation would be that mortality, via weight loss, was due to exclusion from limited resources (Nichols and Haramis 1980, Alexander 1983). Thus the mechanism inducing female mortality remains unclear.

Evidence from these winter observations suggested that differential emigration of females at the onset of winter was the primary mechanism producing a skewed sex ratio in populations of mallards wintering at the latitude of Edmonton which supports the "dominance hypothesis". As Ketterson and Nolan (1979) suggested, this may be the most important cause of differential distribution patterns of the sexes in several species of wintering birds. Overwinter mortality, therefore, may be a secondary mechanism that lowers still further, the proportion of females in a population that is subjected to an extremely severe winter climate. It is unlikely that this mechanism operates on waterfowl wintering in more southerly areas where they are not subjected to such a rigorous climate as that experienced by these populations.

The "dominance hypothesis" suggests that dispersal (in this study: emigration) is caused by intersexual competition for limited resources (Gauthreaux 1978, Ketterson and Nolan 1979). It is unclear whether emigration of females at the onset of winter is caused by direct competition between individuals or is merely a manifestation of the general tendency in birds for females to disperse in greater numbers and over longer distances than males. Whatever the cause, the result appears to be an evolutionary adaptation to avoid mortality caused by thermoregulatory costs and/or competition for resources later in the winter.

LITERATURE CITED

Alexander, W.C. 1983. Differential distributions of wintering diving ducks (*Aythyini*) in North America. Am. Birds 37: 26-29.

Alexander, W.C. 1987. Aggressive behavior of wintering diving ducks (*Aythyini*). Wilson Bull. 99: 38-49.

Anderson, B.W., and R.L. Timkin. 1972. Sex and age ratios and weights of common mergansers. J. Wildl. Manage. 36: 1127-1133.

Bellrose, F.C. 1976. Ducks, Geese and Swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Bellrose, F.C., and R.D. Crampton. 1970. Migrational behavior of mallards and black ducks as determined from banding. Illinois Nat. Hist. Surv. Bull. 30: 167-234.

Bennett, J. W., and E.G. Bolen. 1978. Stress response in wintering green-winged teal. J. Wildl. Manage. 42: 81-86.

Boyd, H. 1964. Wildfowl and other waterfowl found dead in England and Wales in January-March 1963. Wildfowl Trust Ann. Rep. 15: 20-22.

Brodsky, L.M., and P.J. Weatherhead. 1984. Behavioural thermoregulation in wintering black ducks: roosting and resting. Can. J. Zool. 62: 1223-1226.

Calder, W.A. 1974. Consequences of body size for avian energetics. Pp. 86-144 *in* Avian Energetics (R.A. Paynter, Ed.). Nuttall Ornithol. Club Publ. No. 15, Cambridge, Massachusetts.

Dixon, W.J., M.B. Brown, L. Engelman, J.W. France, M.A. Hill, R.I. Jennrich, and J.D. Toporek. 1983. BMDP Statistical Software. University of California Press, Berkeley, California.

Dolbeer, R.A. 1982. Migration patterns for age and sex classes of blackbirds and starlings. J. Field Ornithol. 53: 28-46.

Fretwell, S.D. 1972. Populations in a Seasonal Environment. Princeton Univ. Press, Princeton, New Jersey.

Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. Pp. 17-54 *in* Perspectives in Ethology, Vol. 3 (P.P.G. Bateson, and P.H. Klopfer, Eds.). Plenum Press, New York, New York.

Heitmeyer, M.E. 1985. Wintering strategies of female mallards related to dynamics of lowland hardwood wetlands in the upper Mississippi delta. Unpubl. Ph. D. dissert., University of Missouri, Columbia, Missouri.

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

Jorde, D.G., G.L. Krapu, R.D. Crawford, and M.S. Hay. 1984. Effects of weather on habitat selection and behavior of mallards wintering in Nebraska. Condor 86: 258-265.

Ketterson, E.D., and J.R. King. 1977. Metabolic and behavioral responses to fasting in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). Physiol. Zool. 50: 115-129.

Ketterson, E.D., and V. Nolan Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). Ecology 57: 679-693.

Ketterson, E.D., and V. Nolan Jr. 1979. Seasonal, annual, and geographic variation in the sex ratio of wintering populations of dark-eyed juncos (*Junco hyemalis*). Auk 96: 532-536.

King, J.R., D.S. Farner, and L.R. Mewaldt. 1965. Seasonal sex and age ratios in populations of white-crowned sparrow of the race *gambelii*. Condor 67: 489-504.

Lebret, T. 1950. The sex ratios and the proportion of adult drakes of teal, pintail, shoveler, and wigeon in the Netherlands, based on field counts made during autumn, winter and spring. Ardea 38: 1-18.

Myers, J.P. 1981. A test of three hypotheses for latitudinal segregation of sexes in wintering birds. Can. J. Zool. 59: 1527-1534.

Nelson, H.K. 1978. Effects of the severe winter of 1976-1977 on waterfowl. Int. Waterfowl Symp. 3: 39-44.

Nichols, J.D., and G.M. Haramis. 1980. Sex-specific differences in winter distribution patterns in canvasbacks. Condor 82: 406-416.

Nichols, J.D., K.J. Reinecke, and J.E. Hines. 1983. Factors affecting the distribution of mallards wintering in the Mississippi alluvial valley. Auk 100: 932-946.

Nilsson, L. 1976. Sex ratios of Swedish mallards during the non-breeding season. Wildfowl 27: 91-94.

Nilsson, L. 1983. September and January counts as a measure of changes in south Swedish mallard populations. Wildfowl 34: 89-98.

Nilsson, L. 1984. The impact of hard winters on waterfowl populations of south Sweden. Wildfowl 35: 71-80.

Paulus, S.L. 1983. Dominance relationships, resource use, and pairing chronology of gadwalls in winter. Auk 100: 947-952.

Perdeck, A.C., and C. Clason. 1983. Sexual differences in migration and winter quarters of ducks ringed in the Netherlands. Wildfowl 34: 137-143.

Prince, H.H. 1979. Bioenergetics of postbreeding dabbling ducks. Pp. 103-117 *in* Waterfowl and Wetlands - An Integrated Review (T.A. Bookout, Ed.). Proc. 1977 Symp. N. Cent. Sec., Wildl. Society, Madison, Wisconsin.

Reinecke, K.J., T.L. Stone, and R.B. Owen, Jr. 1982. Seasonal carcass composition and energy balance of female black ducks in Maine. Condor 84: 420-426.

Roseberry, J.L. 1962. Avian mortality in southern Illinois resulting from severe weather conditions. Ecology 43: 739-740.

Sayler, R.D., and A.D. Afton. 1981. Ecological aspects of common goldeneyes *Bucephala clangula* wintering on the upper Mississippi River. Ornis. Scand. 12: 99-108.

Smith, H.G., and J. Nilsson. 1987. Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): an evaluation of different hypotheses. Auk 104: 109-115.

Smith, K.G., and H.H. Prince. 1973. The fasting metabolism of subadult mallards acclimatized to low ambient temperatures. Condor 75: 330-335.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. Freeman and Co., San Francisco, California.

Sugden, L.G., W.J. Thurlow, R.D. Harris, and K. Vermeer. 1974. Investigations of mallards overwintering at Calgary, Alberta. Can. Field-Nat. 88: 303-311.

Whyte, R.J., and E.G. Bolen. 1984. Impact of winter stress on mallard body composition. Condor 86: 477-482.

III: DOMINANCE BEHAVIOUR AND ITS CONSEQUENCES IN CAPTIVE MALLARDS

INTRODUCTION

Competition for a limited resource which is critical either for survival or reproductive success is an important mechanism of natural selection, as it can lead to the exclusion of one of the competing individuals from that resource (Lack 1968). Therefore any characteristic that improves competitive ability should be favoured by natural selection. In passerines, dominance status is often associated with superior survival and reproductive success (Fretwell 1969, Kikkawa 1980, Arcese and Smith 1985) and that may also be true of waterfowl (Scott 1980a, Hepp 1984, Heitmeyer 1985, Teunissen et al. 1985, Lamprechet 1986, Alexander 1987). For example, the "dominance hypothesis" which is based on a dominant-subordinate relationship among competing individuals (Gauthreaux 1978) has been used by several authors to explain differential distribution patterns of the sexes in ducks during the winter period (Nichols and Haramis 1980, Sayler and Afton 1981, Hepp and Hair 1984); subordinate females are forced to migrate farther south than dominant males.

Dominance status may affect an individual in several ways: its spatial position within a flock (Swingland 1977, Nichols and Haramis 1980, Weatherhead and Hoysak 1984), its success in mate acquisition (Korschgen and Fredrickson 1976, Scott 1980b, Searcy 1979b, Wishart 1983), and/or its level of body reserves (Fretwell 1969, Patterson 1977, Heitmeyer 1985), presumably through priority of access to food (Paulus 1983, DeLaet 1985).

Many studies have examined dominance status in relation to individual characteristics. In waterfowl, status has been correlated with age (Alexander 1987), sex (Raveling 1970), size (Scott 1980b), weight (Patterson 1977), plumage (Titman and Lowther 1975), and pairing status (Hepp and Hair 1984). There are also indications in other bird species that dominance may be under genetic control and/or is learned from experience as a family member (Boag 1982, Moss et al. 1982, Arcese and Smith 1985).

The evidence suggests that a dominant-subordinate relationship exists in many birds and that there is some advantage to being dominant. But dominance has relevance only when it can provide access to critical resources which are limited in abundance or accessibility (Kaufmann 1983). In these situations a subordinate incurs the cost of exclusion. This concept is a critical assumption inherent to many behavioural studies of waterfowl which document interactions (and therefore competition) between dominant and subordinate individuals (Hepp and Hair 1984, Paulus 1983, Alexander 1983, 1987, Heitmeyer 1985). But if critical resources are not limited, interactions between individuals have little meaning because exclusion cannot occur.

In this study I examined the dominant-subordinate relation among individuals in a flock of captive mallards (*Anas platyrhynchos*) during the winter period. I tested the critical assumption that behavioural interactions over a specific resource (food, loafing space, dabbling space) were an indication that the resource was limited. I also explored several characteristics of the ducks that potentially could influence their dominance status. These included size, weight, sex, pairing status, hatch date, and experience obtained as a sibling. Finally, I assessed the effects of dominance status on an individual's ability to acquire access to a limited resource (loafing space, mates), and on its lipid reserves.

STUDY AREA AND METHODS

The study was conducted from May 1985 to March 1986 at the Brooks Wildlife Centre located near Brooks (50° 35'N, 111° 54' W), Alberta. The facilities used at the center were designed specifically for waterfowl maintenance and production and consisted of a series of enclosed pens separated from one another and covered with wire mesh. This study can be divided into three distinct sections, each with its own methods.

Summer

Eggs from nests of wild mallards were collected near Brooks between May and June, 1985 and incubated at the centre. When dry, the sex of newly hatched ducklings was determined, they were web-tagged, and placed with siblings in an observation pen which measured 1.2 m^2. Each group of siblings was visually isolated from one another, provided with a heat lamp, water, and commercial waterfowl starter ration ad lib, and maintained under a natural photoperiod for a 3-week period. At 4 days of age each duckling was individually marked with an adjustable vinyl neck collar at which time daily observations were begun to establish the nature of dominance relationships within each brood. Aggressive interactions, defined as a peck or bite, were recorded and the number of wins/ total number of interactions within each sex was used to establish the status of the individual (bites directed at the neck collar or web tag were ignored). I assumed that the dominance relationships in the brood at 3 weeks of age remained stable for the duration of the study (Balph 1979, Gregoire pers. comm.). After 3 weeks observations were terminated, the neck collars removed, and the broods placed in larger outdoor pens. A 2.6 m^2 pond, shelter and commercial duck grower (switched to maintenance ration at 6 weeks of age) was provided ad lib. Individual broods were physically but not visually isolated. Just before fledging, primaries on the left wing were clipped to prevent flight.

Winter (outdoor)

In early October, 1985 each mallard was given a numbered leg band and a coded vinyl nasal saddle (Sugden and Poston 1968). On October 15 (and at 2-week intervals thereafter), birds were weighed to the nearest 25 g using a 2 kg Pesola spring scale. On October 15, 18 males and 18 females, randomly selected from the entire flock (196 birds), were placed into one of four pens. This procedure was repeated three more times to give 36 mallards in each of four pens for a total of 144 birds. On December 17, 6 females were randomly selected from each pen and then removed to bring the total in each pen to 30 birds to simulate the skewed sex ratio typical of this species (Bellrose 1976).

Each pen was 150 m², contained a 10 m² section of pond, a 6 m² loafing platform covered in straw and was visually isolated from other such pens. Water was kept ice free with a 200 watt stock pond heater and occasional removal of ice. Ponds were drained, cleared and refilled every 5 days. Commercial duck maintenance ration and hard wheat in a ratio of 7:3 were provided ad lib using three gravity flow self-feeders each with an aperture measuring 10 cm in diameter. Daily food consumption was measured by volume to the nearest 100 ml.

On November 21, the amount of food available in two of the four pens was reduced to create restricted diet treatment and thereby reduce the level of endogenous reserves of the treated birds below those of birds given an ad lib diet. This involved removing two of the three feeders and reducing food available to 70% of the average daily consumption measured in the two remaining ad lib treatment pens. This amount was further reduced to 60% on December 19 and then to 50% on March 18. Pens 1 and 4, chosen randomly, received the restricted diet whereas Pens 2 and 3 remained on the ad lib diet. Ducks were fed 1 hour before regular observation periods. The area of the loafing platforms in Pens 1 and 4 were also limited by reducing the surface area of straw on each platform by 25%. Ducks used only the straw covered area of each platform.

Beginning on November 8, daily behavioural observations were made from an elevated blind which provided a complete view of two pens. During a fixed 2-hour sampling period (10:00-12:00 or 13:00-15:00) five 10-minute observation sessions were alternated between each of two pens (one treatment and one control). Morning and afternoon sampling periods were alternated for each pen to avoid bias. From January 22 to March 21 the observation time was doubled by using two observers.

During each 10-minute session several data were recorded. Agonistic interactions were noted. For each interaction in which a clear winner and loser could be identified, the initiator, winner, loser, and activity of the non-initiator were noted. To monitor use of loafing areas each platform was divided into 16 blocks of equal size. When an identifiable individual used the platform its identity, position, and the number of individuals on the platform at that time were recorded. Male courtship activity was quantified by recording number of displays exhibited by each male during the observation session. Three displays were used to indicate courtship: the "grunt-whistle", "tail-up, head-up" and the "down-up" display (Johnsgard 1960). Because some displays were missed during periods of intense activity the data represent minimum numbers of displays expressed by any given individual. Pairing was noted; individuals were considered paired if a female showed consistent preference for one male via "inciting behaviour" (Johnsgard 1960), and the male showed no aggressiveness towards that female for at least a 6-day period. This stringent requirement prevented incorrect identification of ephemeral liaisons as pairings. Permanent pairs were defined as those pairs which did not break up during the course of the study, temporary pairs being defined as those that did after being recorded as paired.

Winter (indoor)

In October 1985, 20 individuals (10 males, 10 females) were selected randomly from the remnant of the summer flock and placed in one of two indoor pens. The selection process was then repeated for the second pen. Each pen was maintained at room temperature under natural photoperiod and was 50 m^2 with a 1.5 m^2 pond. Ducks in one pen were provided with commercial duck maintenance ration ad lib using two gravity flow self feeders. Food consumption by ducks in this control pen was monitored on a daily basis to the nearest 50 ml and the ducks in the restricted diet treatment pen were given 50% of amount consumed by the control group. Pens were cleaned once every 2 days. After a 7-week period, feeding was terminated and after 12 hours the birds on the restricted diet were killed, tagged, and frozen. During the study, few courtship displays and no paired birds were observed in the restricted diet treatment pen.

Lipid extraction was conducted on whole carcasses (primaries removed) homogenized twice through a meat grinder with a 5 mm sieve plate. Lipid content of each individual was based on three replicate dried samples (2-3 g) taken from each carcass and determined by a 3-hour Soxhlet extraction using petroleum ether. Maximum differences between replicates was < 4%. Percent lipid content was obtained by dividing the lipid content weight by the dried sample weight.

Data analysis

To examine the influence of resource limitation on interaction rate the numbers of interactions over food, loafing space and dabbling space in each pen were tabulated for two sample sessions. The first session included 10 observation periods (November 8 - November 22) in which all pens received identical non-restricted treatments. The second period contained 14 observation periods (November 23 - December 18) during which two pens (Pens 1 and 4) received reduced amounts of food and loafing space (restricted treatment) and two pens (Pens 2 and 3) received amounts similar to the first sample session (control). These data sets were compared using a G-test for heterogeneity.

Dominance status of an unpaired individual was estimated by dividing the number of wins by the total number of interactions recorded for that individual involving that sex. A win is defined as any interaction in which the individual is deferred to. Because interactions did not occur at random, the number occurring between the sexes being much less then expected (Table III-1), the sexes were considered separately when calculating

Table III-1: Frequency of aggressive interactions between mallards of a given sex(es) observed in each pen during the study.

Comparison	Pen 1		Pen 2		Pen 3		Pen 4	
	Observed	Expected[2]	Observed	Expected	Observed	Expected	Observed	Expected
Male-male	378	218.0	450	219.5	442	223.0	330	193.0
Male-female	148	299.0	103	301.0	115	306.5	128	265.0
Female-female	98	107.0	74	106.5	81	108.5	94	94.0
Probability[1]	<0.001		<0.001		<0.001		<0.001	

[1] Probability based on G-test for goodness of fit.

[2] Expected frequency = (Number of dyads for a given combination of individuals /number of all dyads) X (Total number of observed interactions).

Number of male-male dyads = 160, male-female dyads = 216, female-female dyads = 78.

dominance status. Interactions used in this analysis were derived from regular observation periods plus any interactions observed outside these periods. The accuracy of this estimate depends on the number of observations gathered per bird (Arcese and Ludwig 1986); therefore, when calculating correlation statistics, each pair of values (X, X) was weighted by multiplying it by the number of observations the dominance estimate was based upon. Only those dominance estimates based on ≥ 5 observations were used for all other analyses.

To examine characteristics that may have influenced dominance status simple G-tests were performed on the number of wins for each categorical group (e.g. male vs female). A G-test of independence was used to examine the relationship between dominance status achieved as an individual in a brood to status achieved as an adult. For this analysis dominants are defined as those birds winning greater or equal to the median proportion of wins for that sex. Spearman's coefficient of rank correlation was used to test for significant relationships between continuous variables. It was expected a priori that heavier, larger and earlier hatched individuals would be dominant; hence one-tailed probabilities were used.

Preferential use of specific areas on the platform (edge vs non-edge) by specific categorical groups (e.g. paired males) was examined using a simple G-test. Edge was defined as that portion of the platform (4 of 16 blocks) located adjacent to the pond. The remainder of the straw covered platform was termed non-edge. To ensure these data reflected situations when competition existed for loafing space, data were used in the analysis only when ≥ 8 individuals were on the platform.

To reduce the influence of variable levels of endogenous reserves caused by the diet regime only the control pens (2 and 3) were used in the analysis of courtship data. Courtship was quantified by recording the number of displays expressed by the individual and dividing them by the total number of observation periods in which the bird displayed. Spearman's coefficient of rank correlation was used to test for significant relationships between status of single males and courtship amount, initial date of courtship, and pairing date. The influence of dominance on the permanence of pair bonds and the number of permanent pair bonds of dominant and subordinate individuals was examined by using a G-test for independence. The relationship between percent lipid content and sex, was tested using ANCOVA. Lipid and dominance data were arcsine transformed prior to analysis.

All statistical tests follow Sokal and Rohlf (1981). Spearman's rank correlation and simple linear regression analysis and most ANOVAS were done using the BMDP computer package (Dixon et al. 1983). Nested ANOVA was done using the SAS computer package (SAS Institute Inc. 1985). William's correction factor was used for all G values (Sokal and Rohlf 1981).

RESULTS

Criteria for dominance

The sex and pairing status of the individual affected its dominance status (Table III-2). Under control conditions (Pens 2 and 3), when males, both paired and single, interacted with single females the males won significantly more interactions. Paired males also dominated paired females. But single males were not dominant to paired females (Table III-2). Thus, pairing elevated the dominance status of females from subordinate to one of relative equality with single males. Comparisons within a given sex (Table III-3) showed that paired males dominated single males. Furthermore, the degree of permanency of the pair bond did not influence the dominance status of males; permanently paired males did not win significantly more interactions than temporarily paired males during altercations between these two groups (Table III-3). The results for paired females versus single females

Table III-2: Number of wins recorded during encounters between the sexes of mallards in specific pair-status categories.

	Pen	Single male	Single female	P[1]	Paired male	Single female	P	Paired male	Paired female	P	Single male	Paired female	P
Control	2	90	25	<0.001	7	1	0.029	138	72	<0.001	72	81	0.469
	3	81	47	0.003	29	13	0.013	62	32	0.002	45	56	0.274
Experimental[2]	1	83	65	0.139	21	7	0.007	83	16	<0.001	61	26	<0.001
	4[3]	65	38	0.008	4	11	0.070	50	30	0.025	33	35	0.445

1 Probability based on simple G-test.
2 Reduced availability of food and loafing space (see Methods).
3 Data obtained from female number 05 removed from analysis because of its aberrant aggressive behaviour.

Table III-3: Number of wins associated with specific comparisons of pair status within each sex.

	Pen	Paired[1] male	Single male	P[2]	Permanently paired male	Temporarily paired male	P	Paired female	Single female	P
Control	2	239	96	<0.001	26	32	0.432	5	4	0.746
	3	193	54	<0.001	28	17	0.101	21	10	0.048
Experimental[3]	1	139	135	0.815	27	47	0.020	5	8	0.412
	4	143	150	0.688	30	30	1.000	3	9	0.083

[1] There was no difference between permanently and temporarily paired males versus single males so the data was combined.

[2] Probability based on simple G-test.

[3] Reduced availability of food and loafing space (see Methods).

were inconclusive probably because of the low number of encounters observed (Table III-3). Thus among mallards under control conditions, males dominate females and paired birds dominate single birds, with the possible exception of females.

The relationships are less clear-cut when resources were limited (Pens 1 and 4). Between sex comparisons (Table III-2) show that during agonistic encounters both paired and single males dominated single females, although not all differences were significant. However, paired males won significantly more of the interactions during encounters with paired females. In contrast, single males dominated paired females in one pen but not the other (Table III-2). Comparisons within a sex reveal that paired males did not dominate single males (Table III-3). The small number of observed interactions between paired and single females led to inconclusive results. In the experimental pens males tended to dominate females but paired birds did not dominate single birds, at least among males.

Over the entire study period, a total of 624 (Pen 1), 627 (Pen 2), 638 (Pen 3) and 552 (Pen 4) aggressive interactions involving single birds was observed. There were no consistently significant relationships between phenotypic characteristics (body weight, wing chord, tarsus and culmen length) and dominance status of single birds within either sex in either the control or experimental groups (Table III-4). By contrast, significantly negative relationships between hatch date and dominance status were observed in females (Table III-4), suggesting that the later a female hatched the lower its dominance status. No relationship, however, was observed between the dominance status (proportion of wins) of an individual within a brood and that shown as an adult for either males or females (Table III-5).

Frequency of interactions

The number of agonistic interactions occurring within any given 4-day period varied over time in all four pens (Fig. III-1). More interactions occurred in the experimental group

Table III-4: Spearman's coefficients of rank correlation for dominance status (proportion of wins) and phenotypic characteristics among captive mallards. Only those coefficients for which $P < 0.10$ are probabilities of a one-tailed test indicated in parentheses (n = 18 males, 12 females).

Sex		Pen	Body weight[1]	Flattened wing chord	Tarsus length	Culmen length	Hatch date
Male	Control	2	0.097	0.439 (0.036)	0.303	-0.370	0.296
		3	0.166	0.219	0.011	-0.398	-0.047
	Experimental[2]	1	-0.135	-0.409	-0.304	0.017	-0.105
		4	0.414 (0.043)	0.398 (0.051)	-0.301	0.092	-0.235
Female	Control	2	-0.075	0.274	0.357	-0.020	-0.770 (0.002)
		3	-0.289	0.030	0.075	0.510 (0.029)	-0.508 (0.029)
	Experimental	1	0.266	0.167	0.667 (0.006)	0.584 (0.012)	-0.441 (0.072)
		4	0.135	0.376	0.199	0.167	-0.832 (<0.001)

[1] Body weight at beginning of study.

[2] Reduced availability of food and loafing space (see Methods).

Table III-5: Relationship between dominance status of mallards as adults versus as ducklings for males and females. Values represent number of individuals (Pens 2 and 3, and 1 and 4 combined).

	Male				Female			
Duckling	Adult Control		Adult Experimental[1]		Adult Control		Adult Experimental	
	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate
Dominant	8	6	8	5	6	5	6	4
Subordinate	7	8	8	7	2	3	3	3
Probability[2]	0.572		0.661		0.589		0.697	

[1] Reduced availability of food and loafing space (see Methods).
[2] Probability based on G-test of independence.

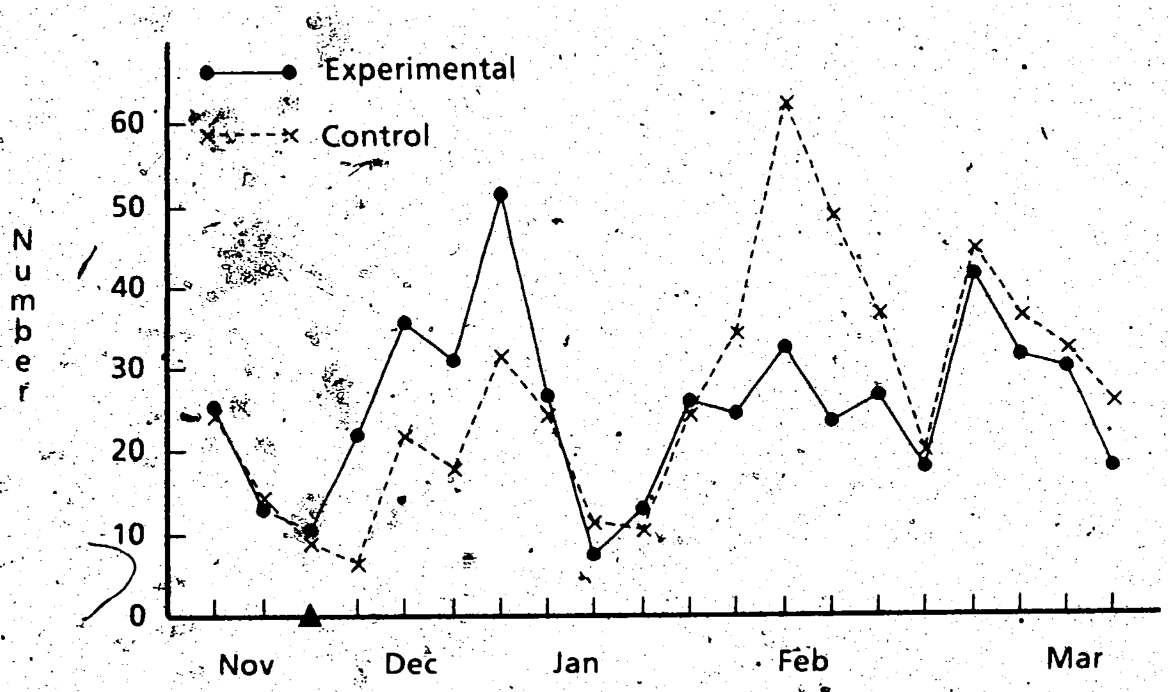


Figure III-1: Number of agonistic interactions recorded among captive mallards within 4-day periods from Nov. 8 to Mar. 21. (Pens 1and 4, 2 and 3 combined). Experimental conditions initiated on Nov. 23, involved reduced availability of food and loafing space (see Methods).

than the control group prior to mid-January, but the reverse occurred after this time. However, statistical analyses of the data for these two periods (Table III-6) shows that these differences approached, but did not reach, significance in both cases.

Because of variation in the number of interactions for loafing space over time (e.g. Fig. III-1) and the absence of interaction data for food after December 19 (food was consumed before behavioural observations commenced) analyses of loafing and feeding data was confined to the first part of the study period. For the data recorded from November 8 to December 18 (start of reduced resource abundance occurred on Nov. 23), distinct trends are apparent. Of the 436 aggressive interactions tabulated for all four pens the majority involved three activities: access to 1) space on loafing platforms (47.8%), 2) dabbling space on water (32.8%), and 3) space at the feeders (16.7%). The number of interactions involving these specific activities was markedly influenced by resource abundance (Fig. III-2). Before food and space were reduced the number of interactions recorded in all pens was low. Thereafter the number of interactions rose more in the experimental pens, where the birds were subjected to reduced amounts of food and availability of loafing space, than in the control pens where numbers of interactions remained relatively stable (Fig. III-2a-b). A statistical analysis of the food and loafing data showed that significant heterogeneity existed between the four pens which was attributable to differences between the experimental and control groups (Table III-7). In contrast to the results for feeding and loafing the number of agonistic interactions during dabbling activities (Fig. III-2c) showed no significant change (Table III-7). Since the water space provided by each pond was limited (minimum area for each duck = 0.27m^2), but constant, it is not unreasonable that interaction rates should have remained relatively constant.

Table III-6: Mean (± SD) number of aggressive interactions among mallards within 4- day periods during the study before and after Jan. 6.

	Pen	Number of Interactions[1]	
		Nov.23-Jan.6	Jan.7-Mar.21
Control	2	23.4 ± 13.6 (5)[4]	34.5 ± 15.4 (12)
	3	17.6 ± 7.7 (5)	30.3 ± 17.9 (12)
Experimental[2]	1	34.4 ± 11.1 (5)	23.2 ± 9.2 (12)
	4	32.2 ± 13.7 (5)	25.1 ± 11.4 (12)
Probability[3]		$0.05 < P < 0.10$	$0.05 < P < 0.10$

[1] Number of interactions = mean number for all interactions recorded over 6.7 hours of observations within a 4- day period.
[2] Reduced availability of food and loafing space (see Methods).
[3] Probability based on mixed model nested ANOVA.
[4] Sample size

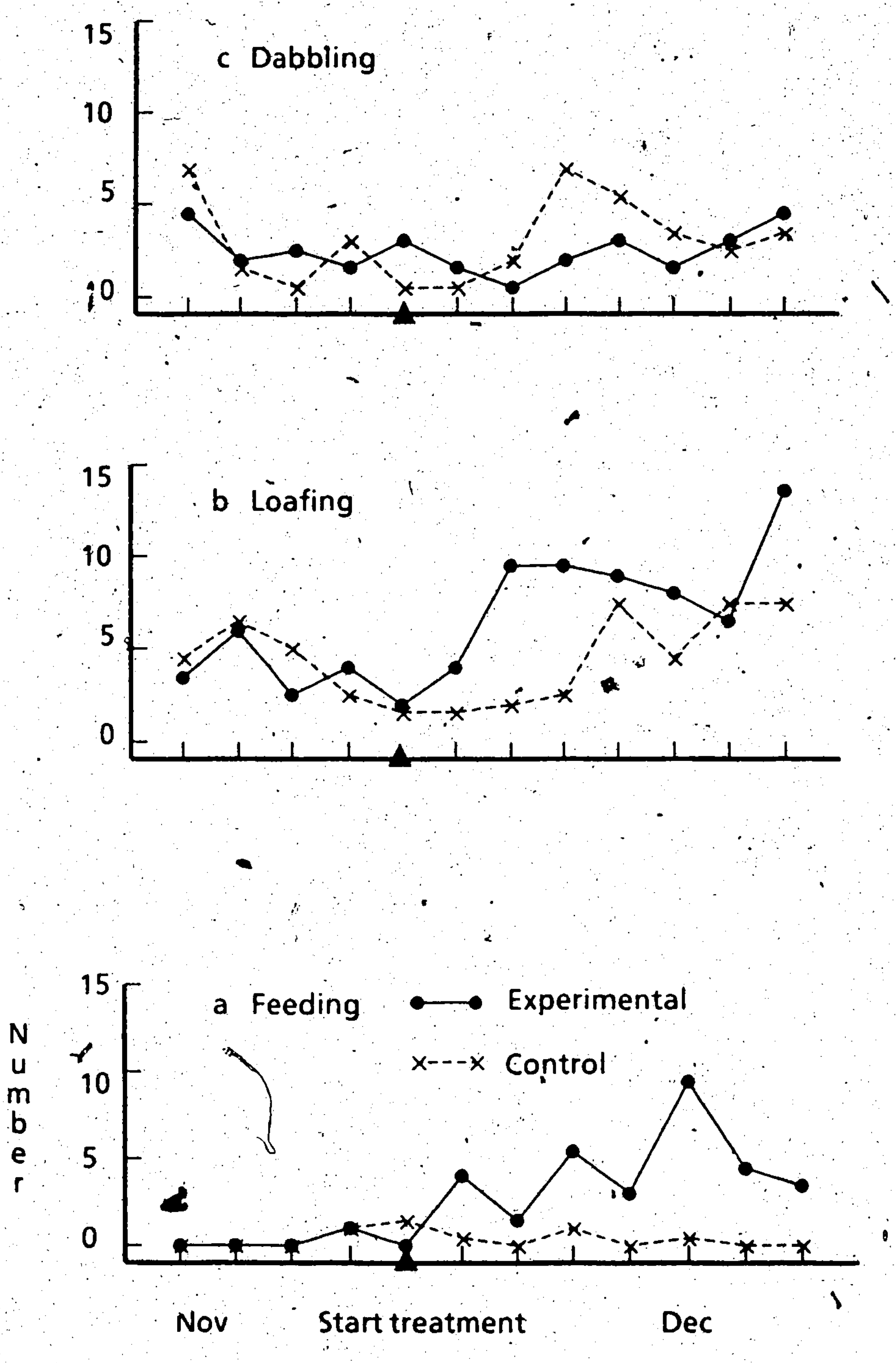


Figure III-2: Number of agonistic interactions recorded among captive mallards during 2-day periods before and after the availability of food and space was reduced (see Methods) on Nov. 23 in the experimental groups a: feeding activity, b: loafing c: dabbling

Table III-7: Number of agonistic interactions recorded among captive mallards while involved in specific activities before and after reduction of resources on Nov. 23.

	Pen	Feeding		Loafing		Dabbling	
		Before[1]	After[2]	Before	After	Before	After
Control	2	2	3 A[4]	30	28A	15	27 A
	3	3	2A	10	11 A	10	22 A
Experimental[3]	1	1	26 B	27	60 B	14	13 A
	4	1	37 B	7	32 C	10	15 A
Probability[5]		<0.001		<0.001		0.120	

1 Each pen observed for 10 sample periods prior to reduced treatment (Nov.8-22).
2 Each pen observed for 14 sample periods during reduced treatment (Nov.23 - Dec.18).
3 Reduced availability of food and loafing space (see Methods).
4 Different letters identify pens which are not homogenous (Unplanned tests for homogeneity; $X^2_{0.05[6,1]} = 6.92$, based on Sidak's multiplicative inequality).
5 Based on G-test for heterogeneity among pens.

Influence of dominance

Loafing

To ascertain whether dominance status was related to use of preferred areas on the loafing platforms it was first necessary to demonstrate that preferred areas existed. During observations it quickly became apparent that the edge of the platform closest to the pond was used more frequently than the remainder of the platform. Analysis of distribution patterns for males (Table III-8) and females (Table III-9) verified these observations, in that a preference was shown for the pond edge when < 8 individuals were present (low competion). The pond edge was used (and therefore assumed to be preferred) more often than the non-pond edge of the platform.

When ≥8 individuals were present on the platform, and space was not reduced (control Pens 2 and 3), positions used on the platform were dependent on dominance status of both males (Table III-10) and females (Table III-11). Subordinate single males used the pond edge less than expected whereas paired males used this area more than expected. The distribution of dominant single males did not differ significantly from that expected based on availability. Dominant single females and paired females also used the pond edge more than expected(Table III-11).

Results are not as clear for the experimental group (Pens 1 and 4). Subordinate single males did not use the pond edge less than expected and dominant single males used the pond edge more than expected only in Pen 4 as did paired males in Pen 1 (Table III-9). For females (Table III-11), dominant and subordinate single birds, and paired females used the pond edge more than expected only in Pen 1.

Table III-8 : Frequency of positional use of loafing platform by groups of male mallards of different dominance status when < 8 individuals are on platform.

	Pen	Dominant single males			Subordinate single males			Paired males		
		Pond edge	Non-pond edge	P1	Pond edge	Non-pond edge	P	Pond edge	Non-pond edge	P
Control	2	13	8	<0.001	20	9	<0.001	29	19	<0.001
	3	15	13	0.002	16	12	<0.001	23	9	<0.001
Experimental2	1	14	13	0.028	15	12	0.019	27	31	0.037
	4	13	4	<0.001	12	11	0.056	16	9	0.003

1 Probability based on simple G-test.
2 Reduced availability of food and loafing space (see Methods).

Table III-9: Frequency of positional use of loafing platform by groups of female mallards of different dominance status when < 8 individuals are on platform.

	Pen	Dominant single female			Subordinate single female			Paired female		
		Pond edge	Non-pond edge	P[1]	Pond edge	Non-pond edge	P	Pond edge	Non-pond edge	P
Control	2	—	—[3]		—	—		34	19	<0.001
	3	5	1	0.004	6	5	0.040	6	8	<0.001
Experimental[2]	1	11	6	0.009	6	1	0.004	22	23	0.032
	4	11	5	0.004	7	5	0.077	14	5	<0.001

[1] Probability based on simple G-test.
[2] Reduced availability of food and loafing space (see Methods).
[3] Insufficient data for analysis.

Table III-10: Frequency of positional use of loafing platform by groups of male mallards of different dominance status when ≥ 8 individuals are on platform.

	Pen	Dominant single males			Subordinate single males			Paired males		
		Pond edge	Non-pond edge	P[1]	Pond edge	Non-pond edge	P	Pond edge	Non-pond edge	P
Control	2	9	23	0.690	2	31	0.004	48	76	0.001
	3	23	53	0.495	13	68	<0.001	50	102	0.030
Experimental[2]	1	26	40	0.295	21	36	0.555	42	54	0.034
	4	10	11	0.027	9	19	0.400	10	13	0.303

[1] Probability based on simple G-test.

[2] Reduced availability of food and loafing space (see Methods).

Table III-11: Frequency of positional use of loafing platform by groups of female mallards of different dominance status when ≥ 8 individuals are on platform.

	Pen	Dominant single female			Subordinate single female			Paired female		
		Pond edge	Non-pond edge	P[1]	Pond edge	Non-pond edge	P	Pond edge	Non-pond edge	P
Control	2	7	2	0.001	—[3]	—		31	57	0.046
	3	11	5	<0.001	12	20	0.121	36	24	<0.001
Experimental[2]	1	14	8	0.004	8	5	0.041	31	30	0.005
	4	3	6	0.665	—	—		7	9	0.384

[1] Probability based on simple G-test.
[2] Reduced availability of food and loafing space (see Methods).
[3] Insufficient data for analysis.

Courtship and pairing success

Very little overt aggression was observed between male mallards during courtship activities ($< 3\%$ of all interactions). Dominance status was not correlated with the initial date of courtship activity (Table III-12). However, displaying rate was negatively correlated with dominance status in Pen 2 and the relationship between dominance status and date of pair formation was also negatively correlated in both Pens 2 and 3. Thus the more dominant a male was the less it courted (Pen 2) and the earlier it paired.

The number of permanent pairs formed by male mallards, although not significantly dependent on status, did show a tendency towards dominant males forming a greater proportion of the pair bonds (Table III-13). Permanence of pair bonds was independent of dominance status (Table III-14). Successful pairing does not appear to depend on dominance status of the individual.

Lipid reserves

The percentage of lipid reserve in 10 male (36.4 ± 6.7) and 10 female (35.6 ± 9.7) mallards, housed indoors to remove the influence of extreme cold, were not different (Table III-15). An individual's level of lipid reserves at the end of a period of reduced resource availability was not related to sex. Thus, for this flock of birds, it appears that dominance status was not related to lipid reserves even in the face of limited food availability.

It was assumed a priori that males would dominate females during aggressive interactions over food. This status would provide priority of access to the resource, which in turn, would be reflected in higher lipid reserves in males than females, at the end of the study. Males won significantly more interactions than females when the two sexes interacted ($P < 0.01$) but the number of interactions occurring between the sexes was

Table III-12: Spearman's coefficients of rank correlation between dominance status of male mallards and their courtship and pairing activity.

Pen	Initial date of courtship	P[1]	Courtship amount[2]	P	Pair date	P
2	-0.061 (18)[3]	>0.05	-0.586 (15)	<0.05	-0.578 (12)	<0.05
3	0.194 (18)	>0.05	0.108 (16)	>0.05	-0.800 (9)	<0.01

1 Probability.
2 Number of courtship displays/number of observation periods in which individual displayed.
3 Sample size.

Table III-13: Comparison of the dominance status[1] of male mallards with the number of pairs[2] formed (Pens 2 and 3 combined).

Status	Paired		Probability[3]
	Yes	No	
Dominant	9	6	0.208
Subordinate	6	10	

[1] Individuals with <5 interactions removed from analysis.
[2] Pairs defined as those which are permanent.
[3] Probability based on G-test of independence.

Table III-14: Comparison of the dominance status[1] of male mallards with permanence of their pair bonds (Pens 2 and 3 combined).

Status	Permanent		Probability[2]
	Yes	No	
Dominant	9	1	0.396
Subordinate	6	2	

[1] Individuals with <5 interactions removed from analysis.
[2] Probability based on G-test of independence.

Table III-15: ANCOVA on percent lipid content data (arcsine transformed) obtained from 10 male and 10 female mallards subjected, as a group, to reduced food abundance. Dominance status (arcsine transformed) within each sex used as covariate.

Source	df	Sums of squares	Mean squares	F value	Probability
Equality of adj. means	1	14.533	14.533	0.302	0.585
Zero slope	1	1328.701	1328.701	27.630	<0.001
Error	57	2741.106	48.090		
Equality of slopes	1	0.011	0.011	0.000	0.988
Error	56	2741.096	48.948		

much less than expected ($P < 0.001$). Thus, although males were dominant to females, females appeared to avoid interactions with males. Furthermore, if lipid reserves of females at the start of the study were greater than those of the males, then the final lipid levels would not reflect accurately, the influence of dominance. The body condition indices (body weight/flattened wing chord) of males and females at the beginning of the study however, were not statistically different (t-test; $t = 1.69$, $df = 19$, $P > 0.10$). Finally, if males had priority of access to food this probably would be reflected by the rate of weight loss of each sex during the study. No differential rates of weight loss between the sexes was observed (ANCOVA, $F = 0.326$, $P = 0.513$). Ad hoc observations made during feeding periods support these results. No clear defence by individuals of the resource was recorded at any time. Instead a frenzied scramble by all individuals for the food was observed, which precluded efficient defence of the resource.

Although dominance status did not affect the rate of weight loss or the level of lipid reserves at the end of the study between the sexes, a significant linear correlation ($P < 0.001$) did exist within each sex (Figure III-3). Lipid reserve levels of an individual at the end of the study was related to its dominance status within that sex.

DISCUSSION

Criteria for dominance

Among several species of waterfowl, sex and pair status are frequently used as determinants of dominance; males are said to dominate females, and paired birds are said to dominate single birds (Paulus 1983, Raveling 1970, Hepp and Hair 1984). In this study male mallards dominated females and paired birds dominated single birds when availability of food and loafing space were not restricted. These relationships did not hold, however, when the resources were restricted; paired males did not dominate single males. This cannot be attributed to the influence of interactions recorded for any single activity as

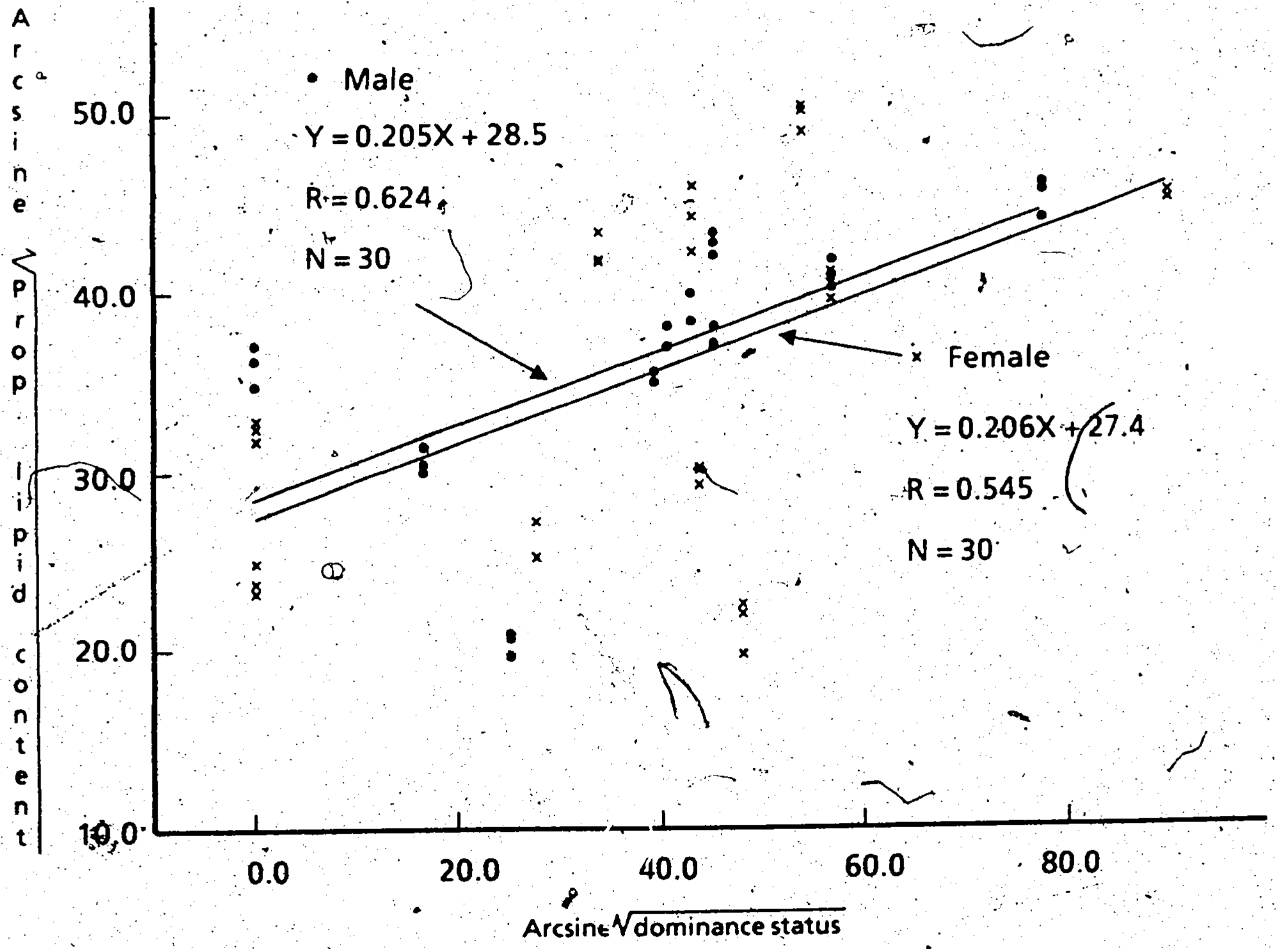


Figure III-3: Relationship between dominance status (number of wins/ number of interactions within the sex) and percent lipid content in a flock of male and female captive mallards on a restricted diet regime (3 replicates / individual).

this result was similar for all activities. One explanation, that the dominance status of males forming temporary pair bonds was insufficient to dominate single males, was not true. Possibly, when a resource is limited the motivation of individuals to acquire the resource may rise and therefore the dominant-subordinate relationship may break down (Parker 1974a). Also, birds in these pens were in relatively poor condition (see Chapter 4) which could also have influenced the relationship, or it may simply reflect a chance event.

Paired females did not dominate single males which contrasts with the observations of Paulus (1983) for gadwall (*Anas strepera*), Heitmeyer (1985) for mallards, and Hepp and Hair (1984) for several other *Anas* spp. In those wild populations paired females dominated single males. My results may reflect a captive situation where individual recognition and learned status could have lessened the effect of paired status. Still, paired females achieved a higher dominance status (neutral) than that of single females (subordinate).

To identify criteria that may determine dominance within a sex, three attributes (morphology, experience, and age) were tested. Despite the suggestion that large size may enhance dominance status in birds (Searcy 1979a), recent studies that have controlled for the correlation between size and other variables (e.g. sex, age) have found no such relationships (Kikkawa 1980, Davies and Lundberg 1984, Arcese and Smith 1985). The results for the Anatidae are ambiguous. This study found no relationship between size and dominance status nor was one found in either adult (Raveling 1970) or gosling (Gregoire pers. comm.) Canada geese (*Branta canadensis*), but a positive correlation was found between these variables in Bewick's swans (*Cygnus columbianus*) by Scott (1978) cited in Scott (1980b). Intuitively one would expect large size to be advantageous during aggressive encounters which are used to assess dominance, but the results of this study do not support this expectation.

Prior experience may be an important factor which can influence dominance status of the individual (Immelmann 1975, Baptista et al. 1987). In Japanese quail (*Coturnix coturnix*) status achieved as a brood mate can in part affect an individual's status as an adult (Boag 1982). In this study no relationship existed between status achieved as a brood mate and status as an adult, which is similar to the findings of Arcese and Smith (1985) for juvenile song sparrows (*Melospiza melodia*). As suggested by Boag (1982) and Moss et al. (1982) aggressiveness as an adult may be explained by heritability and not entirely by learning through early experience. Also, it was assumed that brood mates would maintain stable dominance relationships as has been observed in other young birds (Balph 1979, Boag and Alway 1981, Gregoire pers. comm.). But, if the status of ducklings in this study, recorded during early life, were not stable, these results cannot be interpreted with any confidence. More work is needed in this area before any conclusions can be made pertaining to mallards.

The final attribute thought to influence dominance within a sex was age (or hatch date). Although adult ducks often dominate juveniles (Paulus 1980, Alexander 1987) few studies have investigated the effect of age within a year-class. In this study a significant negative correlation between hatch date and dominance existed in female mallards and a nonsignificant trend was found for males. This relationship was also observed by Arcese and Smith (1985) in juvenile song sparrows and surprisingly, as in this study, hatch date was the only significant predictor of dominance among individuals within a sex. Garnett (1981) found that among captive great tits (*Parus major*) older juveniles dominated younger ones as did Kikkawa (1980) for yearling grey-breasted silvereyes (*Zostercops lateralis*). Two possible explanations exist for this phenomenon. First, experience, as proposed by Arcese and Smith (1985), allows an individual to acquire fighting skills through participation in aggressive encounters. This is an unlikely scenario for these captive mallards as discussed above. Also, while development of fighting skills may occur, status within the brood is also being learned. Consequently, a duckling which continuously loses interactions may also be learning that it is subordinate. A second and possibly related reason for the correlation between hatch date and dominance status is the level of hormone production as mediated through variation in sexual maturity.

Several studies have documented the effects of androgen levels on aggressive behaviour in birds (e.g. Etienne and Fisher 1964, Balthazart and Stevens 1975, Akessen and Raveling 1981, Balthazart 1983) and it has been shown that sexual maturity will affect hormone production (Akessen and Raveling 1981, Balthazart 1983). During his investigation of dominance in chickens, Rushen (1982) found that a linear hierarchy formed in relation to differences in maturation dates. Earlier-maturing males were dominant to their later-maturing companions. As well, the initial status depended on the age of first aggressiveness while the final (stable) status depended on the age of first being submitted to by another individual. Although the relationship between hormone levels, aggression and maturation are extremely complex (Dittami and Reger 1984) it is conceivable that earlier-hatching ducks have a higher hormone production on a given date than their later-hatching companions. These potentially more aggressive ducks would have a greater chance of becoming dominant. This explanation may also apply to adult birds at different stages of the reproductive cycle(e.g. paired vs single birds) or in different states of body condition.

The results of this study show that males dominate females, paired birds dominate single birds and within female mallards at least, dominance is correlated with hatch date. For many social animals that live in small groups and form relatively stable hierarchies, individual recognition can also be used to assess status. However, most waterfowl species which winter in north temperate regions reside in large unstable flocks (Bellrose 1976) precluding the possibility of individual recognition or the formation of dominance hierarchies (Raveling 1970). Yet in the wild, aggressive interactions occur in waterfowl and dominant-subordinate relationships exist (Paulus 1983, Hepp and Hair 1984, Alexander [illegible]87). This raises the following question :how can these stable dominance relationships exist without continuous aggressive altercations over resources? A possible explanation may be status-signalling.

Status-signalling as defined by Rohwer (1975) is a means by which the social status of an individual can be assessed on the basis of its plumage. The occurrence of status signaling has been documented for several bird species (Rohwer 1975, Ketterson 1979, Ewald and Rohwer 1980, Parsons and Baptista 1980, Jarvi and Bakken 1984). Plumage variability, not individual recognition, is used to assess status. Because of the large size and instability of winter flocks (Rohwer 1975) status-signalling may be an important cue for deciding dominance status during interactions among waterfowl. Sexually dimorphic plumage characteristics occur in many duck species (Bellrose 1976) and in the same way, paired status can be used as an indicator of dominance status. Problems exist with this mechanism for mallards in that yearlings are subordinate to adults (Heitmeyer 1985), but have similar plumage. Moreover, paired individuals are dominant to other individuals during interactions away from their mates (pers. obs.). It is possible, however, that subtle variations in plumage or behavioural postures, as suggested by Heitmeyer (1985), may be important.

As stated by Ketterson (1979) the presence of characteristics which are good predictors of dominance status does not demonstrate that a bird species employs status-signalling, but it could provide a simple explanation for the presence of dominant-subordinate relationships in mallards without the occurrence of continual overt aggressiveness.

Interaction frequency

Aggressive interactions over resources have been observed in several species of waterfowl during the winter period (Patterson 1977, Paulus 1983, Hepp and Hair 1984, Heitmeyer 1985, Alexander 1987). All of these studies suggest that aggressive interactions reflect competition for a finite resource, with exclusion of some individuals from that resource. But, for competition to be effective the resource need only be defendable; it may or may not be finite in abundance (Davies and Houston 1984). If interactions occur for resources which are not limited in abundance, exclusion cannot occur and aggressive interactions observed in wild duck populations may have little meaning.

The results from this study suggest that aggressive interactions will not occur for a resource that is not limited in abundance (food) and a reduction in the abundance of a resource (food and loafing space) will increase the frequency of interactions over that resource. These results are similar to those reported by Davies and Houston (1981, 1984) for the pied wagtail (*Motacilla alba*). Defence of a food resource by an individual was abandoned during periods of super abundance because intruders did not affect its feeding rate, but as food abundance declined the individual would vigorously defend the resource and oust any intruders. When provided with a predictable, high quality food source the birds in this study appeared simply to wait for access to the food or move away at the approach of an intruder. But when food abundance was reduced aggressive interactions ensued. The number of interactions over space on the loafing platform was also related to resource abundance. A decrease in loafing area was associated with an increase in the number of interactions for that space. Space on the loafing platform was limited in abundance at all times but the number of interactions was dependent on the degree of resource limitation. Comparable results were found for a winter population of European blackbirds (*Turdus merula*) by Lundberg (1985). Interaction rates were generally very low with the exception of two peaks, one, just before fall migration and the second, when food abundance was reduced.

Caution should be used when applying this interpretation to wild populations of waterfowl. For example, wild birds have a time constraint associated with feeding which is virtually nonexistent for captive birds (e.g. < 2% of observation time recorded as feeding in control pens). Despite being abundant, a food resource to a wild bird may still be limited simply because of the nature of the resource (e.g. its caloric value) and time constraints placed on the bird (Brodsky and Weatherhead 1985, Paulus 1982). With this in mind it appears that aggressive interactions for food in a flock of captive mallards will occur only when the resource is limited in abundance and that the number of interactions for loafing space can be increased by a reduction in the available space. These results support the suggestion that aggressive interactions which occur in wild populations represent competition for resources which are limited in abundance. If true, the question becomes, can the individual be excluded from some critical resource and can it suffer some adverse effects from this exclusion?

Influence of dominance status

Loafing

Position used on the platform appeared to be related to dominance status in that paired birds used the preferred area on the platform more than expected by chance and subordinates males used this area less than expected. Because competition existed between individuals for use of this preferred area, dominant birds should be able to acquire the "best" location and conversely, those individuals of low status should be excluded from it. The results are not conclusive, but this pattern was observed in paired birds and subordinate single males. Exceptions existed for single females, dominant single males in most of the pens, and subordinate single males in the experimental pens, all of which showed either a random pattern of use or use opposite to expected. Because single females avoided interacting with males, it is possible that they used the platform only in the absence of males, but the data recorded precludes analysis of this explanation. Paired males did not dominate single males in the experimental pens which could explain the lack of significance between dominance and position on the platforms in these pens. This reasoning is inappropriate for the control pens. However, the results obtained from the control pens indicated that dominance status did influence positional use of the loafing platforms.

Use of certain positions within a flock has been documented for several other bird species. Murton et al. (1966, 1971) found that among wood pigeons (*Columba palumbus*) individual birds remained in certain positions within the feeding flock. Dominant adult birds were positioned in the middle of the flock and fed at a more rapid rate than subordinate juveniles which were forced to the front of these feeding groups. Juveniles were more vigilant, had lower feeding rates, and were less selective feeders. The authors suggested that these subordinates, which had lower survival rates, could not maintain their body reserves as the result of ineffective feeding and may have suffered higher predation rates. Weatherhead and Hoysak (1984) examined the pattern of roosting red-winged blackbirds (*Agelaius phoeniceus*) in a cattail marsh. Dominant adult males were found in the centre of the roost in the densest vegetation surrounded by subordinate juveniles in sparse vegetation. They suggested that a central position would provide better protection from predation as well as providing a more favourable microclimate to those birds using the dense vegetation. Swingland (1977) observed rooks (*Corvus frugilegus*) during the winter period. Dominant adults chose the highest positions in communal roosting trees but moved to lower levels during periods of extreme cold, presumably to reduce heat loss and at this time the subordinate juveniles were quickly evicted from these sheltered locations. Recently, Brown (1984) reported that dominant purple martins (*Progne subis*) showed preferences for certain positions within the flock.

Jorde et al. (1984) documented use of sheltered locations during extreme cold by mallards in Nebraska. Females did not use these areas as frequently as pairs or males, and the authors suggested that they were forced out by dominant birds. Bailey and Batt (1974) observed interspecific aggression and hierarchies in ducks feeding in association with whistling swans (*Cygnus columbianus*). The most aggressive and largest species exploited the optimal locations. Paulus (1983) observed that paired gadwalls fed in the central locations of flocks and suggested the subordinate single birds were forced to peripheral areas of lower food abundance. This argument has also been used by Nichols and Haramis (1980) and Alexander (1987) in their studies of male and female canvasbacks. Because those individuals that use specific locations (e.g. centre of flock, closer to the water's edge) can be less vigilant than other birds (Jennings and Evans 1980, Inglis and Lazarus 1981, Lendrem 1983), it suggests that these locations provide better protection from predation (Moriarty 1976, Hamilton 1971). Presumably the position closest to a secure site provides the best protection from predation. In this study this preferred location appeared to be the pond edge of the platform. Use of this preferred location, which was limited, resulted in expulsion from it of subordinates. If individuals in peripheral locations suffer higher predation rates than those on preferred (optimal) locations, an ecological advantage exists for dominant individuals.

Courtship activity and pair formation

According to Trivers (1972) the sex making the largest parental investment will be most selective. In many north temperate duck species the female produces and incubates the eggs and provides care and protection to the young until or shortly before fledging (Bellrose 1976). It would appear that females have a greater investment than males and therefore should be more selective during the mating process. Searcy (1979b) suggested that to influence a female's choice, male characteristic(s) must: 1) be variable, 2) must be accurately assessable prior to mating and 3) must ultimately have a significant effect on a female's reproductive success. In some duck species one such factor appears to be dominance (Korschgen and Fredrickson 1976, Wishart 1983). Males also outnumber females in most waterfowl species (Bellrose 1976); therefore female availability may influence a male's reproductive success (Trivers 1972). Consequently, intense competition may occur between males for access to females during courtship and high dominance status would be advantageous during mate acquisition (McKinney 1975, Williams 1983).

It appears that, for captive male mallards, dominance influences courtship amount (Pen 2) but not the initial date of courtship. Male mallards usually display while part of a courtship party consisting of one to several individuals of both sexes (Johnsgard 1960). Inherent to these groups are aggressive interactions between males competing for prospective mates (Weidmann 1971) which may lead to expulsion of some individuals as has been observed in wood ducks (Armbruster 1982). If this occurs in mallards, dominant males should exclude subordinates from the group through aggressive interactions. Males in this study showed little overt aggression that resulted in expulsion and the amount of courtship of single males was negatively correlated with status in one of the study pens (Pen 2). Johnsgard (1960) observed similar results for males with damaged plumage. These individuals displayed more often and for longer periods of time than males with normal plumage, and they never successfully paired. He suggested that because these males were not successful, they were "trying harder" than the males with normal plumage. This explanation may also apply to subordinate single male ~~mallards in~~ this study. The date of pair formation was also correlated with dominance status in both control pens. Because dominant male ~~mallards~~ paired earlier than subordinates and the amount of courtship in Pens 2 and 3 was reduced during the early part of the study (see Chapter 4) the negative correlation between dominance status and courtship amount in single male mallards (Pen 2) probably reflects this relationship rather than that between dominance status and amount of courtship.

Position within the courtship party may also influence pairing success (McKinney 1975). Simmons and Weidmann (1973) found that male mallards "aim" their displays at specific females and dominants may in fact achieve the best positions (Weidmann and Darley 1971, Standen 1980). Although this parameter was not quantified it was apparent from ad hoc observations that males would "jockey" for position to display to specific females. Therefore dominance status may affect the effectiveness of displays which could reduce the need for a high display rate and allow dominant males to pair earlier. The amount of courtship a male exhibits has been found to influence pairing success in mallards (Bossema and Kruit 1982); therefore dominance may influence pairing date indirectly through its effect on courtship activity, although the results just discussed would refute this suggestion. As a result of his study of pairing in adult and juvenile black ducks (*Anas rubripes*), Hepp (1986) suggested that dominance may be involved in the timing of pairing and ultimately pairing success.

Although the mechanism is unclear, it appears then, that dominance provides the means by which a male can pair at an earlier date relative to subordinate males. Because strong competition for mates decreases the availability of unpaired females pressure to pair early would increase (Parker 1974b). Birds pairing early would have a longer period of time to test mate quality and if necessary seek another mate prior to breeding (Wishart 1983).

If dominance status can be used as an accurate measure of male "quality" and to provide access to females during intense competition, that would be reflected in the permanence of the pair bond. Halliday (1983) suggests that females should mate with dominant males to reduce problems of harassment. In ducks, a female is guarded by its vigilant mate against other courting males and predators (McKinney 1975), allowing the female to feed with less disturbance (Paulus 1980, Ashcroft 1976). Because many pair bonds are ephemeral in ducks (McKinney 1970) and mate preference has been observed in the mallard (Lebret 1961) and other ducks (Korschgen and Fredrickson 1976, Wishart 1983), presumably dominance will influence a males effectiveness and therefore its ability to maintain the bond. In situations of intense competition for mates (this study) dominant males should maintain pair bonds more successfully than subordinates. For captive male mallards in this study no significant relationship was found between dominance status and permanence of the pair bond. Because some unpaired dominant males were present throughout the study period, the lack of competition directed towards paired subordinate males is not a likely explanation for these results. Energetic constraints are an important aspect of pair bond maintenance (see Chapter 4). It is suggested that once a female chooses a mate this factor rather than male dominance affects the permanence of the bond.

Courtship activity, pairing chronology and permanence of the pair bond all affect pairing success of a male. For captive male mallards in this study a nonsignificant relationship was found between dominance status and the tendency to form pairs. In two other studies of captive waterfowl, dominant male wood ducks (Korschgen and Fredrickson 1976) and American wigeon (Wishart 1983) were more successful in forming pair bonds than subordinates.

Although dominance status was correlated with the amount of courtship and pairing date, it was not correlated with a male's ability to acquire a mate or its ability to maintain that bond. Both, ultimately, affect pairing success and therefore reproductive success. It appears that some factor other than dominance influences pairing success.

Lipid reserves

It has been suggested for waterfowl that dominance status, mediated through priority of access to critical resources, may influence an individual's body reserves and/or survival (Nichols and Haramis 1980, Sayler and Afton 1981, Jorde et al. 1984). Several studies of non-waterfowl species have found correlations between status, foraging success and body reserves (Fretwell 1969, Murton et al. 1971, Swingland 1977, DeLaet 1985, Lundberg 1985) but few exist involving ducks. Dominance was directly related to foraging success in a winter population of mallards which were provided with limited defendable food resources (Harper 1982). Paulus (1983) and Alexander (1987) both presented data which showed use of preferred foraging locations by dominant individuals. It has been suggested by Wishart (1983) for wild American wigeon and Heitmeyer (1985) for wild mallards, that a positive relationship exists between dominance (pair status) and body reserves.

The results from this study do not support the suggestion that dominance status influences the level of an individual's body reserves through priority of access to food resources which are limited in abundance. Males did not have higher lipid reserve levels than females, nor was the rate of weight loss significantly different between the sexes. From ad hoc observations of these birds during feeding, these results are not surprising. Priority of access did not exist because of the swamping effect of individuals using the feeder. Despite being dominant, males could not defend the resource due to the large number of competitors. This phenomenon has also been documented by Burger and Gochfield (1984) in gulls. Therefore the design of this experiment may explain the results. Whether dominance status can influence lipid reserve levels of ducks has yet to be answered.

Differences in lipid reserve levels were not related to dominance status between the sexes, but within each sex a significant correlation existed. Differential access to the food resource probably do not explain these results (see above text). Social stress has been used to explain differential survival rates in wild animals (Christian 1971) and inhibition of reproduction in several species of birds (Robel 1972, Crawford 1977, Hannon et al. 1982). Stress has long been accepted as the single most important factor influencing domestic animal health, particularly in poultry such as waterfowl (Hillman et al. 1985). In this study social stress may have had a significant impact on the mallards housed indoors because subordinates had little opportunity to escape from dominants. Danzter and Mormide (1983) suggest that physiological aspects of the environment are powerful activators of endocrine responses which in turn influence the animal's health. Pronounced changes in endocrine activity can occur in subordinates after being subjected to overt aggression; even simple perception of a threat is enough to cause a large change in hormone production (Seyle 1956, Arnore and Dantzer 1980). Because interactions within each sex occurred more often and interactions between the sexes less often then expected ($P < 0.001$) the influence of social stress may explain the correlation between status and lipid reserve levels within each sex. It is conceivable that social stress may also operate in wild populations of ducks. But, much more work is needed in this area of study before any inferences can be made. These results do however illustrate the complex nature of dominance and its influence on the individual.

LITERATURE CITED

Akesson, T.R., and D.G. Raveling. 1981. Endocrine and body weight changes of nesting and non-nesting Canada geese. Biol. Rep. 25: 792-105.

Alexander, W.C. 1983. Differential distributions of wintering diving ducks (*Aythyini*) in North America. Am. Birds 37: 26-29.

Alexander, W.C. 1987. Aggressive behavior of wintering diving ducks (*Aythyini*). Wilson Bull. 99: 38-49.

Arcese, P., and D. Ludwig. 1986. Improving estimates of dominance based on ratios. Condor 88: 106-107.

Arcese, P., and J.N. Smith. 1985. Phenotypic correlates and ecological consequences of dominance in the song sparrow. J. Anim. Ecol. 54: 817-830.

Armbruster, J.S. 1982. Wood duck displays and pairing chronology. Auk 99: 116-122.

Arnore, M., and R. Dantzer. 1980. Does frustration induce aggression in pigs? Appl. Anim. Ethol. 6: 351.

Ashcroft, R.E. 1976. A function of the pairbond in the common eider. Wildfowl 27: 101-105.

Bailey, R.D., and B.D.J. Batt. 1974. Hierarchies of waterfowl feeding with whistling swans. Auk 91: 488-493.

Balph, M.H. 1979. Flock stability in relation to social dominance and agonistic behavior in wintering dark-eyed juncos. Auk 96: 714-722.

Balthazart, J. 1983. Hormonal correlates of behaviour. Pp. 221-365 *in* Avian Biology, Vol VII (D.S. Farner, J.R. King, and K.C. Parkes, Eds.). Academic Press, New York, New York.

Balthazart, J., and M. Stevens. 1975. Effects of testosterone propionate on the social behaviour of groups of male domestic ducklings *Anas platyrhynchos* L. Anim. Behav. 23: 926-931.

Baptista, L.F., B.B. DeWolfe, and L. Avery-Beausoleil. 1987. Testosterone, aggression and dominance in Gambel's white-crowned sparrow. Wilson Bull. 99: 86-91.

Bellrose, F.C. 1976. Ducks, Geese and Swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Boag, D.A. 1982. How dominance status of adult Japanese quail influences the viability and dominance status of their offspring. Can. J. Zool. 60: 1885-1891.

Boag, D.A., and J.H. Alway. 1981. Heritability of dominance status among Japanese quail: a preliminary report. Can. J. Zool. 59: 441-444.

Bossema, I., and J.P. Kruit. 1982. Male activity and female mate acceptance in the mallard (*Anas platyrhynchos*). Behaviour 79: 313-324.

Brodsky, L.M., and P.J. Weatherhead. 1985. Variability in behavioural response of wintering black ducks to increased energy demands. Can. J. Zool. 63: 1657-1662.

Brown, C. 1984. Light-breasted purple martins dominate dark-breasted birds in a roost: implications of female mimicry. Auk 101: 162-164.

Burger, J., and M. Gochfield. 1984. The effects of relative numbers on aggressive interactions and foraging efficiency in gulls: the cost of being outnumbered. Bird Behav. 5: 81-89.

Christian, J.J. 1971. Population density and reproductive efficiency. Biol. Reprod. 4: 248-294.

Crawford, R.D. 1977. Breeding biology of year old and older female red-winged and yellow-headed blackbirds. Wilson Bull. 89: 73-80.

Dantzer, R., and P. Mormede. 1983. Stress in farm animals: a need for reevaluation. J. Anim. Science 57: 6-18.

Davies, N.B., and A.I. Houston. 1981. Owners and satellites: the economics of territory defence in pied wagtail, *Motacilla alba*. J. Anim. Ecol. 50: 157-180.

Davies, N.B., and A.I. Houston. 1984. Territory economics. Pp. 148-169 *in* Behavioural Ecology: An Evolutionary Approach (J.R. Krebs, and N.B. Davies, Eds.). Blackwell Scientific Publications, Oxford, England.

Davies, N.B. and A. Lundberg. 1984. Food distribution and variable mating system in the dunnock, *Prunella modularis*. J. Anim. Ecol. 53: 895-912.

DeLaet, J.F. 1985. Dominance and anti-predator behaviour of great tits *Parus major*: a field study. Ibis 127: 372-377.

Dittami, J.P., and H. Reger. 1984. A factor analysis of seasonal, behavioural, hormonal and body weight changes in adult male barheaded geese (*Anser indicus*). Behaviour 90: 114-124.

Dixon, W.J., M.B. Brown, L. Engelman, J.W. Frane, M.A. Hill, R.I. Jennrich, and J.D. Toporek. 1983. BMDP Statistical Software. University of California Press, Berkeley, California.

Etienne, A., and H. Fisher. 1964. Der einfluss von testosteron auf das Verhalten kastrierter Stockenten (*Anas platyrhynchos* L.) und dessen Beeinflussung durch Testosteron. Z. Tierpsychol. 21: 348-358.

Ewald, P.W., and S. Rohwer. 1980. Age, coloration and dominance in nonbreeding hummingbirds: a test of asymmetry hypothesis. Behav. Ecol. Sociobiol. 7: 273-279.

Fretwell, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Juncos hyemalis*). Bird-banding 40: 1-23.

Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among great tits (*Parus major*). Ibis 123: 31-41.

Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. Pp. 17-54 *in* Perspectives in Ethology, Vol.3 (P.P.G. Bateson, and P.H. Klapfer, Eds.). Plenum Press, New York, New York.

Halliday, T.R. 1983. The study of mate choice. Pp. 297-309 *in* Mate Choice (P.Bateson, Ed.). Cambridge University Press, New York, New York.

Hamilton, W.D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31: 295-311.

Hannon, S.J., L.G. Sopuck, and F.C. Zwickel. 1982. Spring movements of female blue grouse: evidence for socially induced delayed breeding in yearlings. Auk 99: 687-694.

Harper, D.G.C. 1982. Competitive foraging in mallards: ideal free ducks. Anim Behav. 30: 575-584.

Heitmeyer, M.E. 1985. Wintering strategies of female mallards related to dynamics of lowland hardwood-wetlands in the upper Mississippi delta. Unpubl. Ph.D. dissert., University of Missouri, Columbia, Missouri.

Hepp, G.R. 1984. Dominance in wintering Anatinae: potential effects on clutch size and time of nesting. Wildfowl 35: 132-134.

Hepp, G.R. 1986. Effects of body weight and age on the time of pairing of American black ducks. Auk 103: 477-484.

Hepp, G.R., and J.D. Hair. 198[illegible]. Dominance in wintering waterfowl (*Anatini*): effects on distribution of sexes. Condor 86: 251-257.

Hillman, P., N.R. Scott, and A. VanTienhoven. 1985. Physiological responses and adaptions to hot and cold environments. Pp. 1-72 *in* Stress Physiology in Livestock, Vol III Poultry. (M.K. Yousef, Ed.). CRC Press, Inc., Boca Raton, Florida.

Immelmann, K. 1975. The evolutionary significance of early experience. Pp. 331-357 *in* Behaviour: Essays in Honor of Professor Niko Tinbergen, FR.S. (G. P. Baerands, C. Beer, and A. Manning, Eds.). Clarendon Press, Oxford, England.

Inglis, I.R., and J. Lazarus. 1981. Vigilance and flock size in brent geese: the edge effect. Z. Tierpsychol. 57: 193-200.

Jarvi, T., and M. Bakken. 1984. The function of the variation in the breast stripe of the great tit (*Parus major*). Anim. Behav. 32: 590-596.

Jennings, T., and S.M. Evans. 1980. Influence of position in the flock and flock size on vigilance in the starling (*Sturnus vulgaris*). Anim. Behav. 28: 634-635.

Johnsgard, P.A. 1960. A quantitative study of sexual behavior of mallards and black ducks. Wilson Bull. 72: 133-155.

Jorde, D.G., G.L. Krapu, R.D. Crawford, and M.A. Hay. 1984. Effects of weather on habitat selection and behavior of mallards wintering in Nebraska. Condor 86: 258-265.

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

Ketterson, E.D. 1979. Status signaling in dark-eyed juncos. Auk 96: 94-99.

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.

Korschgen, C.E., and L.H. Fredrickson. 1976. Comparative displays of yearling and adult male wood ducks. Auk 93: 793-807.

Lack, D. 1968. Bird migration and natural selection. Oikos 19: 1-9.

Lamprecht, J. 1986. Structure and causation of dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). Behaviour 97: 28-48.

Lebret, T. 1961. The pair formation in the annual cycle of the mallard (*Anas platyrhynchos*). Ardea 49: 97-158.

Lendrem, D.W. 1983. Sleeping and vigilance in birds: field observations of the mallard *Anas platyrhynchos*. Anim. Behav. 31: 532-538.

Lundberg, P. 1985. Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. Behav. Ecol. Sociobiol. 17: 185-189.

Mckinney, F. 1970. Displays of four species of blue-winged ducks. Living Birds 9: 29-64.

Mckinney, F. 1975. The evolution of duck displays. Pp. 331-357 *in* Function and Evolution in Behaviour (G. Baerends, C. Beer, and A. Manning, Eds.). Clarendon Press, Oxford, England.

Moriarty, D.J. 1976. The adaptive nature of bird flocks: a review. Biologist 58: 67-79.

Moss, R., A. Watson, P. Rothery, and W. Glennie. 1982. Inheritance of dominance and aggressiveness in captive red grouse, *Lagopus lagopus scoticus*. Aggressive Behav. 8: 1-18.

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

Murton, R.K., A.J. Isaacson, and N.J. Westwood. 1971. The significance of gregarious feeding behaviour and adrenal stress in a population of woodpigeons (*Columba palumbus*). J. Zool. London 165: 53-84.

Nichols, J.D., and G.M. Haramis. 1980. Sex-specific differences in winter distribution patterns in canvasbacks. Condor 82: 406-416.

Parker, G.A. 1974a. Assessment strategy and the evolution of fighting behavior. J. Theor. Biol. 47: 223-243.

Parker, G.A. 1974b. Courtship persistence and female guarding as male time investment strategies. Behaviour 48: 157-184.

Parsons, J., and L. F. Baptista. 1980. Crown color and dominance in the white-crowned sparrow. Auk 97: 807-815.

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

Paulus, S.L. 1980. The winter ecology of the gadwall in Louisiana. M.S. thesis, University of North Dakota, Grand Forks, North Dakota.

Paulus, S.L. 1982. Feeding ecology of gadwalls in Louisiana in winter. J. Wildl. Manage. 46: 71-79.

Paulus, S.L. 1983. Dominance relationships, resource use, and pairing chronology of gadwalls in winter. Auk 100: 947-952.

Raveling, D.G. 1970. Dominance relationships and agonistic behaviour of Canada geese in winter. Behaviour 37: 291-317.

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

Robel, R.J. 1972. Possible role of behaviour in regulating tetraonid populations. Proc. Int. Ornithol. Congr. 15: 121-133.

Rushen, J. 1982. The peck orders of chickens: how do they develop and why are they linear. Anim. Behav. 1129-1137.

Sas Institute Inc. 1985. Sas Introductory Guide 3rd Edition. Cary, North Carolina.

Sayler, R.D., and A.D. Afton. 1981. Ecological aspects of common goldeneyes *Bucephala clangula* wintering on the upper Mississippi River. Ornis. Scand. 12: 99-108.

Scott, D.K. 1980a. Functional aspects of prolonged parental care in Bewick's swans. Anim. Behav. 28: 938-952.

Scott, D.K. 1980b. Functional aspects of the pairbond in winter in Bewick's swans (*Cygnus columbianus bewickii*). Behav. Ecol. Sociobiol. 7: 323-327.

Searcy, W.A. 1979a. Morphological correlates of dominance in captive male red-winged blackbirds. Condor 81: 417-420.

Searcy, W.A. 1979b. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). Am. Nat. 114: 77-100.

Seyle, H. 1956. The Stress of Life. McGraw Hill Book Co., New York, New York.

Simmons, K.E.L., and U. Weidmann. 1973. Directional bias as a component of social behaviour with special reference to the mallard *Anas platyrhynchos*. J. Zool. London 170: 49-62.

Standen, P.J. 1980. The social display of the Chilean teal *Anas flavirostris flavirostris*. J. Zool. London 191: 293-313.

Sugden, L.G., and H.J. Poston. 1968. A nasal marker for ducks. J. Wildl. Manage. 32: 984-986.

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

Swingland, J.R. 1977. The social and spatial organization of winter communal roosting in rooks (*Corvus frugilegus*). J. Zool. London 182: 509-528.

Teunissen, W., B. Spaans, and R. Drent. 1985. Breeding success in brent geese in relation to individual feeding opportunities during spring staging in the Waddensea. Ardea 73: 109-119.

Titman, R.D., and J.K. Lowther. 1975. The breeding behaviour of a crowded population of mallards. Can. J. Zool. 53: 1270-1283.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136-179 *in* Sexual Selection and the Descent of Man (B.Campbell, Ed.). Heinemann, London, England.

Weatherhead, P.J., and D.J. Hoysak. 1984. Dominance structuring of red-winged blackbird roost. Auk 101: 551-555.

Weidmann, U. 1971. The synchronization of signals in the social display of mallards. Rev. Comp. Anim. [illegible] 131-135.

Weidmann, U. and J. Darley. 1971. The role of the female in the social display of mallards. Anim. Behav. 19: 287-298

Williams, [illegible]M. 1983. Mate choice in the mallard. Pp. 297-309 *in* Mate Choice (P. Bateson, Ed.). Cambridge University Press, New York, New York.

Wishart, R.A. 1983. Pairing chronology and mate selection in the American wigeon (*Anas americana*). Can. J. Zool. : 1733-1743.

IV. EFFECTS OF BODY WEIGHT ON COURTSHIP, PAIRING, AND REPRODUCTION IN CAPTIVE MALLARDS

INTRODUCTION

It is generally accepted that birds must satisfy their maintenance requirements before nutritional resources can be allotted to reproduction (King 1974). Consequently, the availability of critical food resources needed to fulfill energetic and nutritional requirements can be an important constraint on individuals during their reproductive cycle. To optimize reproductive output, birds must complete the various stages in the reproductive cycle rapidly, efficiently, and have one stage follow the other in quick succession (Williams and Nichols 1984); any constraint on the individual at one point in the cycle may have repercussions upon the remaining stages.

Most north temperate dabbling ducks (*Anas* spp.) initiate courtship and establish pair bonds on their winter range, well before migrating to the breeding grounds in spring (Bellrose 1976). During winter, variable climatic conditions can cause fluctuations in the availability of both food and aquatic habitat (Fretwell 1972, Heitmeyer 1985) which, in turn, may advance or delay courtship activity (Brodsky and Weatherhead 1985) and pair formation (Hepp 1986). Any delay may impose energetic and/or time constraints on the individual. The formation of a pair bond in waterfowl is behaviourally complex, being costly in terms of both time and energy (McKinney 1970, 1975, Wishart 1983b), and once formed, maintenance of this bond is also energetically costly (Daly 1978). However, these costs can be more than compensated for; a strong pair bond can provide both social and energetic benefits (Ashcroft 1976, McLandress and Raveling 1981, Paulus 1983), which ultimately, may increase reproductive output (Hepp 1984, Milne 1974).

Availability of both food and habitat on the breeding grounds may also affect an individual's reproductive output (Kaminiski and Gluesing 1987). For those species of dabbling ducks, such as mallards (*Anas platyrhynchos*) which arrive and initiate nesting during the early spring (Cowardin et al. 1985), a reduction in food availability at that time, resulting from adverse climatic conditions, may prevent them from acquiring the requisite resources for reproduction, possibly causing a delay in the onset of laying and a decrease in clutch size (Krapu 1979, Krapu and Doty 1979, Krapu et al. 1983 Duncan 1987). Endogenous body reserves stored by the individual before arriving on the breeding grounds may compensate for potential variation in food availability. Levels of these reserves have also been implicated as important determinants of laying date and clutch size (Krapu 1981, Drobney 1982). Smaller clutches generally mean fewer hatched ducklings. Moreover, within a species, later-hatched broods suffer higher rates of mortality (Dow and Fredga 1984, Hill 1984, Toft et al. 1984). It appears, therefore, that any factor that influences either clutch size or laying date may ultimately control reproductive success and hence the fitness of the individual.

Given that time and energy constraints can influence several stages in the reproductive cycle of dabbling ducks and that these stages extend across seasons, one could expect to observe the effect of a constraint in one season on events in the following season. At the species level a correlation exists between the chronology of pairing dates and nesting dates (Weller 1965) and within a species, yearlings tend to pair later, nest later, and lay smaller clutches than adults (Wishart 1983a, Afton 1984, Cowardin et al. 1985). This suggests that within a species pairing chronology influences nesting chronology (Armbruster 1982, Brodsky and Weatherhead 1985, Hepp 1986) and that body reserves acquired before arrival on the breeding grounds could potentially influence reproductive success (Krapu 1981, Paulus 1983, Hepp 1984, Heitmeyer 1985).

In this study, I tested the effects of body weight, a measure of nutrient reserves, on courtship activity, time of pair formation, and extent of pair bond maintenance of mallards during the winter period. I used one age class of mallards in a captive environment, and manipulated food availability during the winter and spring periods to produce variation in the nutrient reserves possessed by the birds. I compared pairing date with laying date. And finally, by examining laying date and clutch size in mallards with and without reduced food resources during the winter and spring, I determined the impact of food availability on these reproductive variables.

STUDY AREA AND METHODS

This study was conducted from May 1985 to June 1986 at the Brooks Wildlife Center located near Brooks (50° 35'N, 111° 54' W), Alberta. The facilities used at the center were designed specifically for waterfowl maintenance and production and consisted of a series of enclosed pens separated from one another and covered with wire mesh. Each pen had a small "pond" and facilities for providing food and shelter to the occupants. Eggs, collected from nests in the wild near Brooks between May 20 and June 30, 1985, were incubated at the center. When dry, the newly hatched ducklings were placed with siblings, in indoor pens. Each group of siblings was provided with a heat source (heat lamp), water and commercial waterfowl starter ration ad lib, and maintained under a natural photoperiod for a 3-week period. After 3 weeks the broods were placed in larger outdoor pens provided with a 2.6 m^2 pond and shelter; commercial duck grower (switched to maintenance ration at 6 weeks of age) was provided ad lib. Individual broods were physically, but not visually, isolated. Just before fledging, the primaries on the left wing were clipped to prevent flight. These birds were the subjects of this study which was divided into two distinct sections, each with its own procedures.

Winter period

In early October, 1985 each mallard was given a numbered leg band and a coded vinyl nasal saddle (Sugden and Poston 1968). On October 15 (and at 2-week intervals thereafter), birds were weighed to the nearest 25 g using a 2-kg Pesola spring scale. On October 15, 18 males and 18 females, randomly selected from the entire flock (196 individuals), were placed into one of four pens. This procedure was repeated three more times to give 36 mallards in each of four pens for a total of 144 birds. On December 18, six females were selected randomly from each pen and then removed to bring the total in each pen to 30 (18 males: 12 females), simulating the skewed sex ratio typical of this species (Bellrose 1976).

Each pen was 150 m² in area, contained a 10 m² section of pond, a 6 m² loafing platform covered in straw and was visually isolated from other such pens. Water was kept ice free with a 200 watt stock pond heater and occasional removal of ice. Ponds were drained, cleared and refilled every 5 days. Commercial duck maintenance ration and hard wheat in a ratio of 7:3 were provided ad lib using three gravity flow self-feeders each with an aperture measuring 10 cm in diameter. Daily food consumption was measured by volume to the nearest 100 ml.

On November 23, the amount of food available in two of the four pens was reduced to create a restricted diet treatment and thereby reduce the level of endogenous reserves of the treatment birds below those of birds given an ad lib diet. This involved removing two of the three feeders and reducing food available to 70% of the average daily consumption as measured from the two remaining ad lib treatment pens. This amount was further reduced to 60% on December 19 and then to 50% on March 18. Pens 1 and 4, randomly chosen, received the restricted diet whereas pens 2 and 3 remained on the ad lib diet. Ducks were fed 1 hour before regular observation periods. Beginning on

November 8, daily behavioural observations were made from an elevated blind which provided a complete view of two pens . During a fixed 2-hour sampling period (10:00-12:00 or 13:00-15:00) five 10-minute observation sessions were alternated between each of two pens (one treatment and one control). Morning and afternoon sampling periods were alternated for each pen to avoid any potential bias. From January 22 to March 21 the observation time was doubled by using two observers.

During each 10-minute session two types of behavioural data were recorded. Male courtship activity was quantified by recording all occurrences of displays exhibited by each male during the observation session. Three displays were used to indicate courtship: the "grunt-whistle", "tail-up, head-up" and the "down-up" displays (Johnsgard 1960). Because some displays were missed during periods of intense activity the data represent minimum numbers of displays expressed by any given individual. Pairing was noted; individuals were considered paired if a female showed consistent preference for one male via "inciting behaviour" (Johnsgard 1960), and the male showed no aggression towards the female for at least a 6-day period. This stringent requirement prevented incorrect identification of ephemeral liaisons as paired birds. Permanent pairs were defined as those pairs that did not break up during the course of the study, temporary pairs being defined as those that broke up after being recorded as paired.

Spring period

On April 3, 1986 all females that had shown evidence of having paired with a male (45) were placed at random in individual breeding pens with their mates. The remaining three females were placed with a male chosen at random from their winter pen (Pen 1: 1 female, Pen 4: 2 females), and also placed in separate breeding pens. This created 24 pairs from each of the treatment and control groups. Each enclosure was 10 m^2, provided partial visual isolation from other pens, and contained a 2.6 m^2 pond and one gravity flow self-feeder. [illegible] artificial nest box containing straw was provided along with a supply of crushed oyster shell ad lib.

By selecting pairs at random from the two winter groups, (treatment and control: 24 in each group), four new treatments (12 pairs in each) were created. The four treatments based on diet were: restricted winter-restricted spring, restricted winter-unlimited spring, unlimited winter-restricted spring, unlimited winter-unlimited spring. The mean consumption per pair per day of commercial duck breeder ration was calculated to the nearest 50 ml by volume for the 24 pairs on the unlimited spring diet treatment. The remaining 24 pairs on a restricted spring diet received 50% of the diet of the unlimited group for 7 days; this amount was increased to 70% thereafter.

Pens were checked daily for the presence of newly-laid eggs. Of 43 hens that laid clutches, 39 used the artificial nest boxes provided (all three females given a mate laid clutches). Clutches were considered normal only when all eggs were laid within a single nest bowl. The date on which the first egg was found in a nest was considered the laying date. The clutch was considered complete 3 days after the last egg was found. The eggs were then removed, placed in an incubator and the pairs removed from the experiment.

Data analysis

To examine the influence of diet restriction on courtship activity, date of courtship initiation, and pairing date, a mixed model nested ANOVA was used. When sample sizes were unequal the Satterthwaite approximation was applied if appropriate. When the intermediate level of the mean squares was nonsignificant the rules for pooling mean squares were followed (Sokal and Rohlf 1981). Because of variance heterogeneity, comparison of courtship activity by single and paired males was done using the Wilcoxon two-sample test. The relationship between diet restriction and pair bond permanence was examined using a G-test for independence with the Williams correction factor (Sokal and

Rohlf 1981). A one-way ANOVA and ANCOVA were used to examine the influence of treatment on laying date and clutch size respectively. It was decided a priori to test for differences in treatment means between unlimited winter-restricted spring and restricted winter-unlimited spring treatment groups. Nested ANOVAS were done using the SAS computer package (SAS Institute Inc. 1985) while all other ANOVAS were done using the BMDP statistical package (Dixon et al. 1983).

RESULTS

Effect of food limitation

Body weight of both sexes changed over time in relation to food restriction for the duration of the winter study (Fig IV-1). On November 20 (left arrow - Fig.IV-1), at the onset of food reduction (70% ad lib), the mean weights of male and female mallards forming the groups to be given a restricted diet tended to be slightly greater than those of the groups to be retained on the unlimited diet (Fig.IV-1). This difference, however, was significant only among females (Table IV-1). From November 20 to December 3 rapid weight loss occurred in both sexes, caused by low temperatures during this period (mean temperatures: max. = -17.0°C ± 4.6; min. = -27.6°C ± 4.8). Despite the reduced food availability the birds on the restricted diet did not lose significantly more weight than those on the ad lib diet (Table IV-1). On December 3 (centre arrow - Fig.IV-1), the amount of food made available to birds on the restricted diet was reduced further to 60% of the level of intake of the group on the ad lib diet. Both the treatment and control groups exhibited rapid weight gain from December 3 to December 18 (Figure IV-1) but those on the restricted diet did not gain as much as those on the ad lib diet (Table IV-1). From December 18 to March 17 both sexes in both the treatment and control groups lost weight at about the same rate (Fig. IV-1) but the birds on the ad lib diet were significantly heavier than those on the restricted diet during this period (Table IV-2). On March 17 (right arrow -

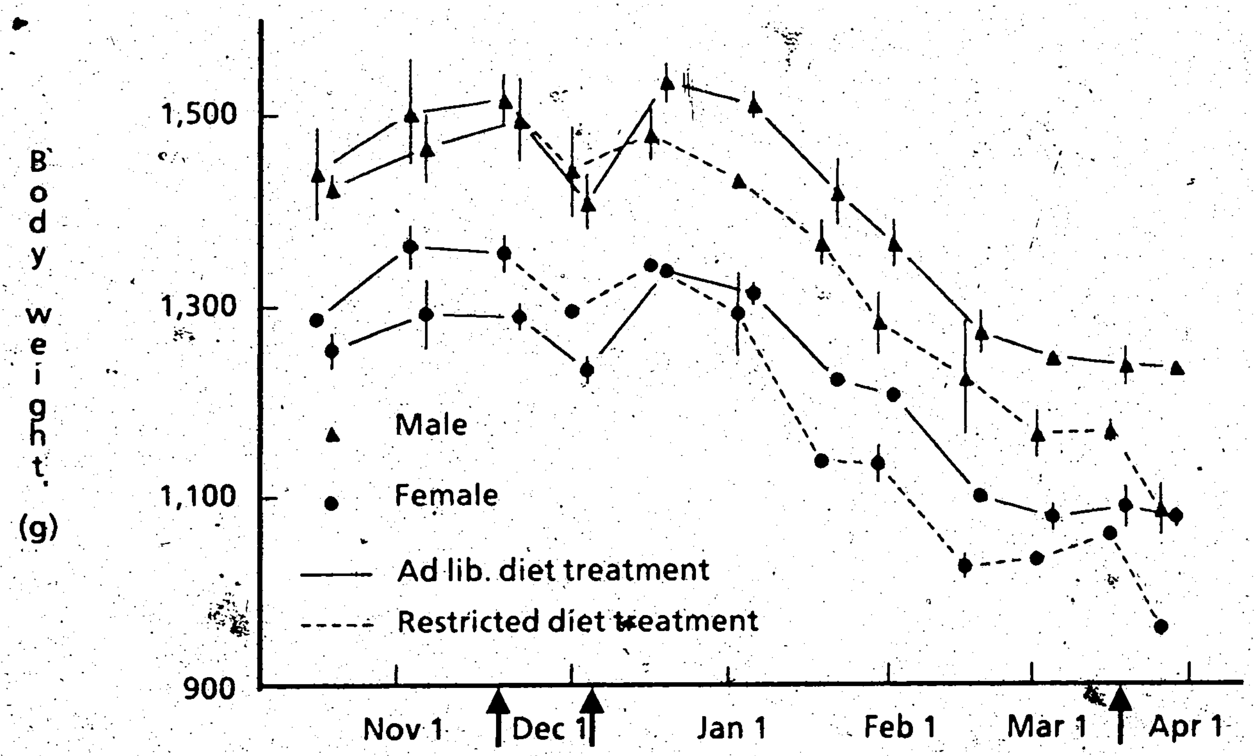


Figure IV-1: Changes over time in mean (± SE) body weight of male and female mallards in relation to diet treatment (replicate pens combined). Arrows represent dates on which diet treatment was altered (see Methods).

TableIV-1: Comparison of mean (± SE) weights (g) and weight changes in captive mallards associated with diet treatment over the winter for each sex. Sample sizes for males = 18; females = 18 to Dec. 18, and 12 thereafter.

Comparison	Female		Difference	Male		Difference
	Ad lib. diet	Restricted diet	P value[1]	Ad lib. diet	Restricted diet	P value
Initial weight (Nov. 20)	1288.3 ± 13.8	1354.4 ± 17.3	<0.05	1494.9 ± 41.1	1515.3 ± 26.2	>0.25
Percent weight loss[2] (Nov. 20-Dec.03)	4.2 ± 0.1	4.3 ± 1.3	>0.30	5.8 ± 0.8	4.8 ± 1.4	>0.50
Percent weight gain[3] (Dec.03-Dec.18)	8.5 ± 1.0	3.5 ± 0.1	<0.05	9.0 ± 0.7	2.4 ± 1.6	0.05<P<0.10
Overall percent weight loss[4] (Nov.20-Mar.27)	16.4 ± 0.1	28.4 ± 1.7	<0.05	17.2 ± 2.0	27.8 ± 0.5	<0.05
Final weight (Mar.27)	1079.8 ± 9.0	964.0 ± 7.7	<0.05	1236.1 ± 4.7	1088.7 ± 26.3	<0.05

1 Based on mixed model nested ANOVA.
2 (weight lost between Nov. 20 and Dec. 03/weight on Nov. 20) X 100.
3 (weight gained between Dec. 03 and Dec. 18/weight on Dec. 03) X 100.
4 (weight lost between Nov. 20 and March 27/weight on Nov. 20) X100.

Table IV-2: Comparison of rate of weight loss among mallards in four pens, and of differences in mean (± SE) body weight (g) between two treatment groups for males and females (Dec. 18 - Mar. 17).

Treatment	Pen	Female		Male	
		Rate of weight loss[2]	Mean body weight[3]	Rate of weight loss	Mean body weight
Restricted diet	1	-4.355	1132.8 ± 11.6	-3.687	1309.4 ± 7.2
	4	-3.648		-3.915	
Ad lib. diet	2	-3.032	1180.0 ± 11.6	-3.772	1369.1 ± 7.2
	3	-4.422		-3.732	
Probability[1]		0.232	0.004	0.968	<0.001

1 Based on ANCOVA.
2 Rate of weight loss tested over 4 pens (Regression coefficient).
3 Mean body weight tested over two treatment groups.

Fig.IV-1), the diet of the restricted treatment group was further reduced to 50% ad lib which induced further weight loss in the experimental groups (Fig.IV-1). At the termination of the winter study, birds on the restricted diet had lost significantly more weight than the birds on an ad lib diet (Table IV-1). From these results it is assumed that for most of the study (December 15 - March 27) the levels of endogenous reserves in individuals of the restricted diet groups were below those of birds on the ad lib diet.

Courtship activity and pairing success

The number of male courtship displays observed in each pen varied considerably among days and between pens (Figs. IV-2 and 3), apparently dependent upon date, climatic conditions, and the pair status of individual males when observations were made. Courtship displays occurred sporadically until the middle of January when a sudden increase was observed which was sustained through to early March (Figs. IV-2 and 3). Even so the number of displays recorded daily fluctuated between days, apparently being influenced by weather conditions; courtship was reduced on days when temperatures fell below -5° C and was eliminated when they fell below -10° C (Fig. IV-4). There is some indication that males given the ad lib diet tended to display more often at colder temperatures than the males given the restricted diet (Fig. IV-4). A male's paired status also influenced courtship activity. In all four pens, males that were permanently paired displayed less frequently than single males or males that formed temporary pairs (Table IV-3). Because of these differences and the fact that each pen did not have the same number of permanently paired males at any given time, data for permanently paired males were omitted from analysis of male courtship activity.

Courtship activity by male mallards did not appear to be affected by diet treatment (Table IV-4). Moreover, comparisons of daily courtship activity for groups observed during the same time period showed no statistical differences (Wilcoxon signed ranks test: Pens 1,

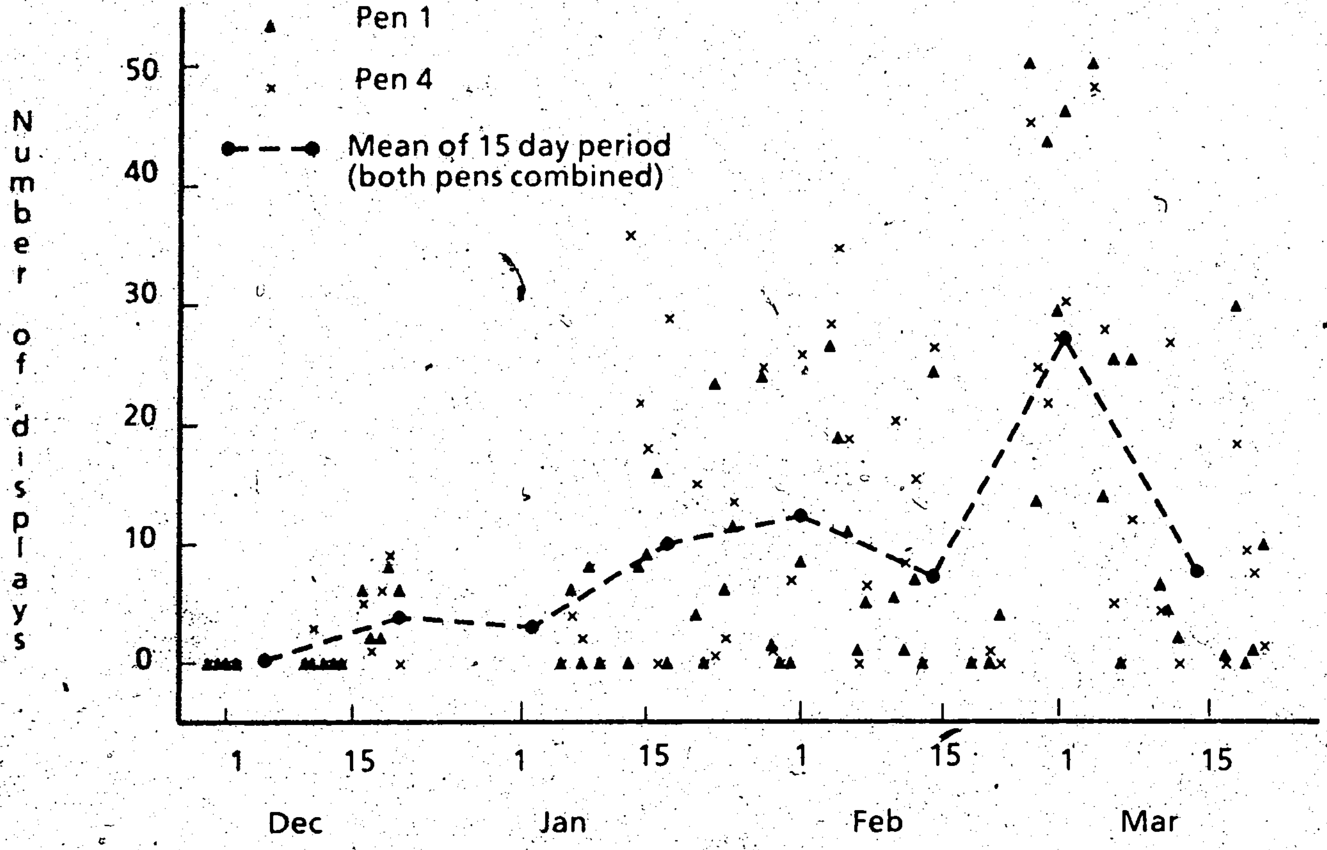


Figure IV-2: Number of courtship displays/day by male mallards observed in pens where birds were given a restricted diet treatment.

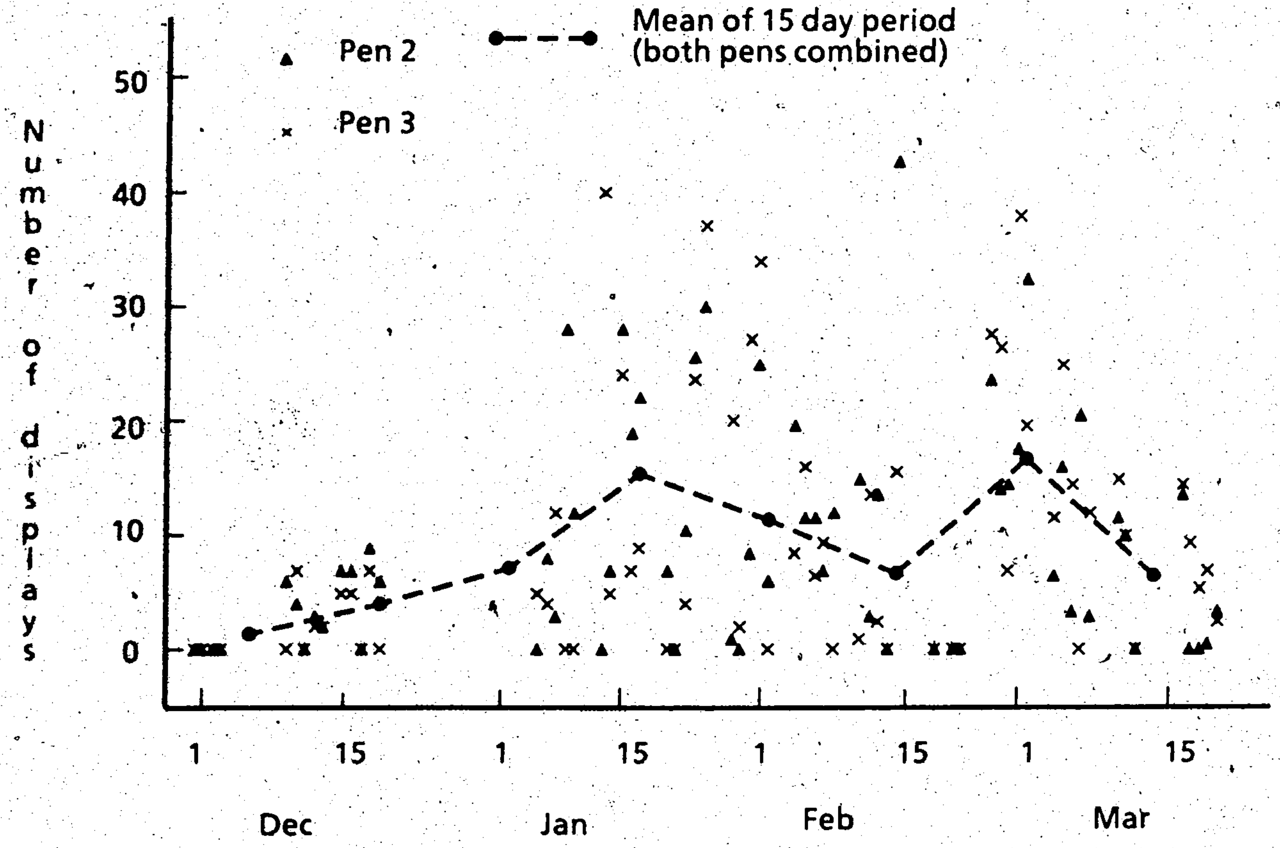
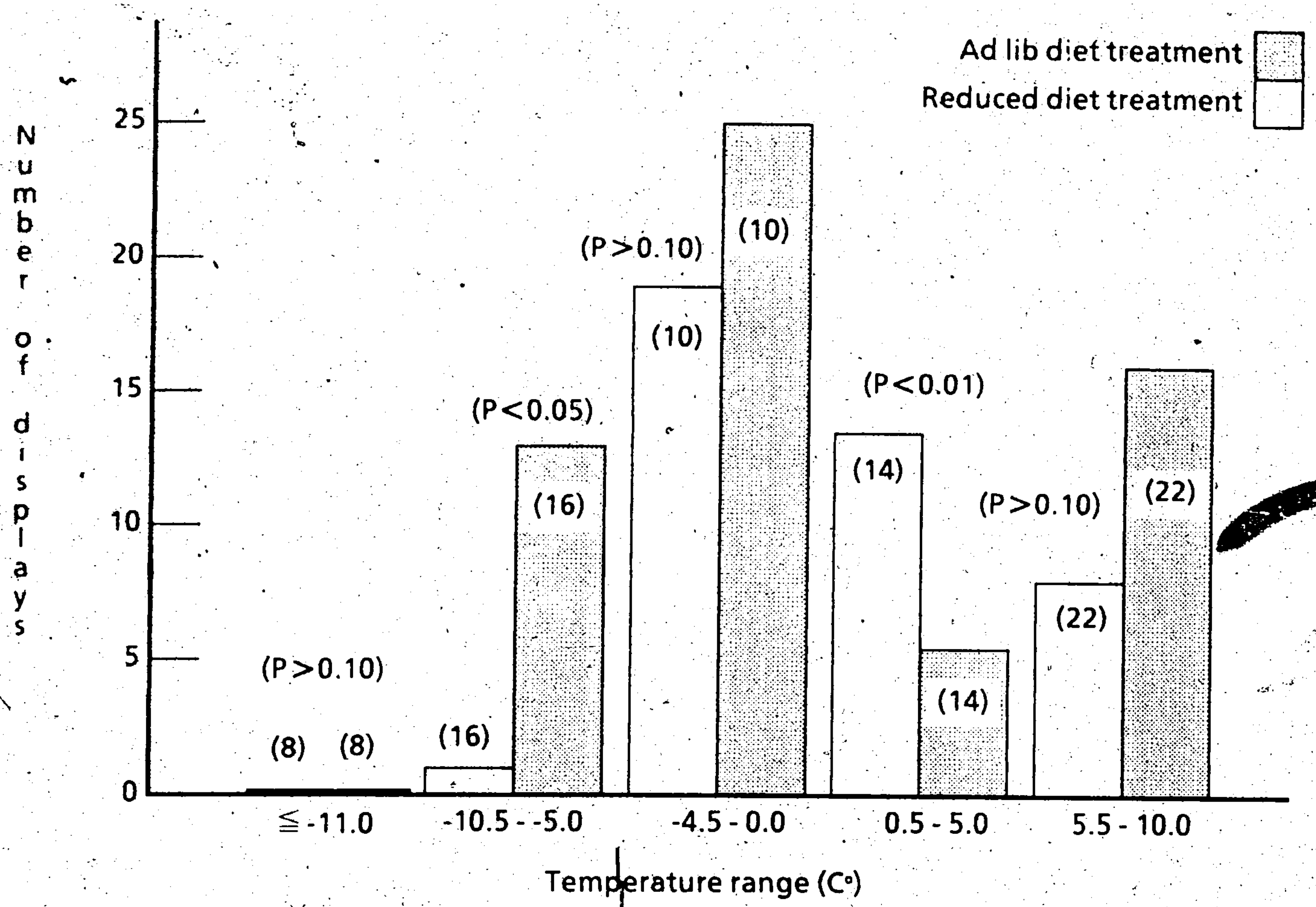


Figure IV-3: Number of courtship displays/day by male mallards observed in pens where birds were given an ad lib. diet treatment.



FigureIV-4: Courtship activity (number of displays/day) of male mallards [median (sample size)] from January 1 to March 20 in relation to five temperature ranges (daily maximum temperature) and two diet regimes (Wilcoxon two-sample test).

8

Table IV-3. Comparison of courtship activity of captive male mallards in relation to their pair and nutritional status.

Treatment	Pen	Courtship amount[1]		Probability[2]
		Permanently paired	Single and temporarily paired	
		Median (n)[3]	Median (n)	
Restricted diet	1	1.280 (6)	1.929 (17)	<0.05
	4	1.136 (5)	2.000 (18)	<0.05
Ad lib. diet	2	1.117 (10)	2.000 (15)	0.05<P<0.10
	3	1.429 (7)	1.775 (16)	<0.05

[1] Courtship amount = number of displays by an individual / number of observation periods in which the individual was actively displaying.

[2] Based on Wilcoxon two-sample test (two-tailed probability).

[3] Sample size.

Table IV-4: Comparison of mean (± SD) rate of male courtship activity, initial date of male courtship, and date of pair bond formation in captive mallards held under two dietary regimes.

Treatment	Pen	Amount ofcourtship by males[1]	Initial date of male courtship[2]	Date of pair bond formation[2]
Restricted diet	1	1.935 ± 0.577(17)[4]	48.8 ± 15.4(18)	84.7 ± 17.9(11)
	4	2.281 ± 0.784(18)	46.1 ± 10.9(18)	92.1 ± 17.0(11)
Ad lib diet	2	2.141 ± 0.790(15)	39.2 ± 10.3(18)	66.5 ± 15.0(12)
	3	2.124 ± 0.928(16)	39.9 ± 8.3(18)	71.4 ± 16.2(9)
Probability[3]		>0.50	<0.05	<0.05

---

[1] Amount of courtship by males = number of displays by males while single or temporarily paired/number of observation periods in which individual was actively displaying (differences between these data and those in TableIV-3 resulted from the elimination of permanently paired males from the analysis - see text).

[2] Number of days since start of observations.

[3] Based on mixed model nested ANOVA.

[4] Sample size.

versus 2, $P > 0.2$; Pens 3 versus 4, $P > 0.3$). Males on the restricted diet displayed as much as males on the ad lib diet. Although no differences were observed in courtship activity of male mallards on two different diet regimes, date of courtship initiation and date of pair formation were different (Table IV-4). Most males on the ad lib diet commenced courtship in mid-December but for males on the restricted diet the onset of courtship displays averaged 8 days later ($P < 0.05$). As well, most pairing took place in mid-January for males on the ad lib diet but males on the restricted diet formed pair bonds on average, 16 days later (Table IV-4).

Most of the 12 females in each pen (1 = 11, 2 = 12, 3 = 9, 4 = 11) paired during the study but the permanence of these pair bonds was influenced by the diet treatment (Table IV-5). Significantly more of the bonds (55%) formed in the groups on a restricted diet were temporary than in the groups (20%) on an ad lib diet.

Reproduction

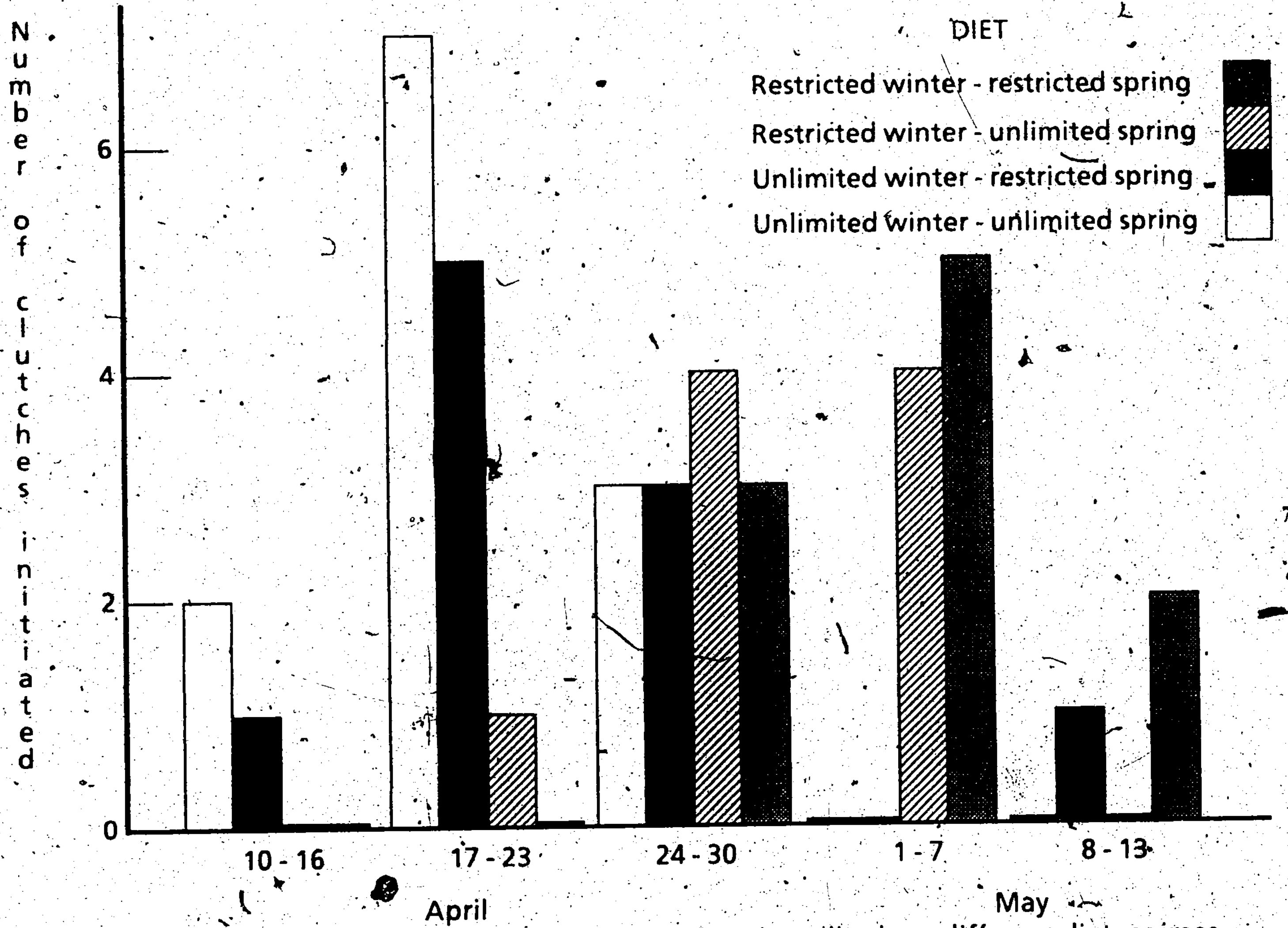
Forty-one of 48 female mallards initiated normal clutches over a 5-week period during the study (Fig. IV-5). A progressively later mean laying date accompanied an increase in the degree of diet restriction. Overall, the mean values of laying dates for the four diet treatments were statistically different (Table IV-6) but more specifically the group on an unlimited winter-limited spring diet initiated nesting significantly earlier than those on the limited winter-unlimited spring diet (Table IV-6). Clutch size did not follow the same trend as laying date (Table IV-6). When the significant correlation ($P < 0.05$) between laying date and clutch size was accounted for no statistical differences existed between the treatment groups. The relationship between date of pairing and laying was also examined, but in none of the four groups was a significant correlation found (Table IV-7).

Table IV-5: Comparison of the number of permanent and temporary pair bonds established by captive mallards relative to their diet regime.

Treatment	Pen	Number of pair bonds		Percent temporary
		Permanent	Temporary	
Restricted diet	1	5	6	54.5
	4	5	6	54.5
Ad lib diet	2	10	2	16.7
	3	7	2	22.2
Probability[1]		$(P<0.05)$		

---

[1] Based on G-test of independence (two replicate pens of diet treatment combined for analysis).



FigureIV-5: Chronology of clutch initiation date among captive female mallards on different diet regimes.

Table IV-6: Comparison of mean (± SD) laying date (number of days since start of treatment) and clutch size of captive mallards on different diet regimes.

Treatment	Sample size	Laying date[1]	Clutch size[2]
Unlimited winter-unlimited spring	12	10.6 ± 3.3	10.7 ± 1.7
Unlimited winter-restricted spring	10	12.9 ± 7.2 A	9.9 ± 1.5
Restricted winter-unlimited spring	9	18.8 ± 4.7 B	11.0 ± 1.5
Restricted winter-restricted spring	10	22.3 ± 4.9	11.0 ± 1.7
Probability		<0.001	0.370

[1] Probability based on one way ANOVA; different letters denote statistically different means ($P<0.05$) based on Planned comparisons F- test.

[2] Probability based on ANCOVA using laying date as covariate.

Table IV-7: Spearman's coefficients of rank correlation between date of pairing and laying in captive mallards on different diet regimes[1].

Treatment	Sample size	r_s	Probability
Unlimited winter-unlimited spring	12	-0.171	>0.05
Unlimited winter-restricted spring	10	0.061	>0.05
Restricted winter-unlimited spring	10	-0.050	>0.05
Restricted winter-restricted spring	10	0.298	>0.05

[1] All pairs which laid normal clutches used in analysis.

DISCUSSION

Courtship activity

The variability in male courtship activity (number of displays per unit time) in each of the groups of male mallards was dependent upon calendar date (photoperiod), climatic conditions (mainly temperature) and individual status (paired or unpaired). In mallards and other dabbling duck species in which most populations winter at more southerly latitudes, courtship usually begins during the fall and early winter (Hepp and Hair 1983, Heitmeyer 1985[illegible]t for those that winter further north, near the northern edge of their winter range, courtship activity is often delayed till late winter (Sugden et al. 1974, Brodsky and Weatherhead 1985). This delay may be attributed to latitudinal differences in day length as photoperiod is a major proximate factor controlling the commencement of courtship activity (Farner and Follet 1979). Inclement weather (low temperatures) during early winter may also delay the commencement of courtship (Lebret 1961). During this study cold temperatures had a dampening effect on the number of displays observed in each group even during periods of peak courtship activity, which is consistent with the observations of Lebret (1961), but contrasts with results found by Brodsky and Weatherhead (1985) who recorded a gradual and constant increase in the amount of time spent courting by male black ducks (*Anas rubripes*) wintering near Ottawa, Ontario regardless of the ambient temperature. Variation between groups was also be caused by the relative numbers of paired and single males in the group that were active on a given day. Several authors have observed the participation of paired and single males in courtship parties (Lebret 1961, Johnsgard 1960), but the degree to which each contributes to courtship activities has rarely been quantified (Williams 1983). In this study males that were single or temporarily paired displayed more often than permanently paired mallards, which is similar to observations made by Turnbull and Baldasarre (1987) of a population of wild mallards. Therefore the number of displays observed on a particular day not only reflected the number of males courting but also the relative abundance of single and paired males in the group. This factor should be taken into account in any study which attempts to quantify male courtship activity, as has been done by Frankel and Baskett (1961) for calling rates of the mourning dove (*Zenaidura macroura*).

Male mallards on a restricted diet commenced courtship displays at a later date than did males on an ad lib diet. These results are consistent with those found by Brodsky and Weatherhead (1985) who found a significant relationship between food abundance at a particular site and commencement of courtship in male black ducks wintering near Ottawa, Ontario. It is generally acknowledged that courtship activity is costly in terms of energy and time (McKinney 1975). If energetic constraints can delay the commencement of courtship one would also expect limitations in the amount of courtship.

Body weight within the range recorded during this study, had no influence on the number of displays expressed by an individual nor was the activity of males on a restricted diet lower than males on an ad lib diet on any given day. Brodsky and Weatherhead (1985) found significant differences between three groups of wild black duck in terms of the percentage of time spent courting. Birds in high quality habitat (high food abundance) spent more time courting than birds residing in areas of low food abundance. They attributed this to differences in body condition and time available for courtship activity (it was assumed that birds in high quality habitat had higher body reserves). My results did not support these conclusions. One reason may be the spatial relationships between groups of mallards in the pens. Because control and treatment pens were adjacent to one another (pens 1 and 2; pens 3 and 4), the amount of courtship by males in each pen may not have been independent of that in the other. It is possible therefore that although visually isolated, males in one pen may have received acoustical stimulation from males in the adjacent pen making the data from adjacent pens nonindependent. Male mallards have been recorded displaying in the absence of females (Johnsgard 1960). Partial correlation coefficients (influence of temperature was removed) calculated for data recorded between January 1 and March 20, however, indicate that this is not the case ($r_{(pens1-2)} = 0.179, P > 0.10$: $r_{(pens3-4)} = 0.116, P > 0.10$). An alternate explanation may be more appropriate: since birds on the restricted diet had ample time available for courtship (little foraging took place after the birds had fed) time rather than energy available for courtship may have been the constraining factor in the Brodsky and Weatherhead (1985) study. It is also possible that the body weights of the males on a restricted diet although low enough to delay commencement of courtship but were not low enough to create significant energetic constraints on the male's ability to display. Another possibility is that the assumption of Brodsky and Weatherhead (1985) about differences in body condition was invalid.

Pair formation and maintenance

As with courtship activity, energetic constraints may govern the timing of pair formation and maintenance of the pair bond (McKinney 1975). In dabbling ducks pairing usually takes place in early winter (Bellrose 1976) but many of these bonds are ephemeral in nature (McKinney 1970). In general, mallards in this study formed pair bonds in mid-January, the timing of which is much later than for wild populations at more southern latitudes (Hepp and Hair 1983). As with courtship activity, pair formation is probably related to photoperiod (Farner and Follet 1979) and influenced by prevailing weather conditions (Lebret 1961). Mallards on a restricted diet, however, paired significantly later than those on the ad lib diet and fewer of the pair bonds were permanent. The differences in chronology of pairing was similar to those found for captive black ducks in southern United States by Hepp (1986). Hepp stated that birds on a restricted diet experienced a delay in pairing relative to that occurring in wild populations at that latitude. The results of this study are not as clear. Birds on the ad lib diet may in fact have paired earlier than wild birds at this latitude (Sugden et al. 1974), which would suggest that such wild birds are food limited. Supplemental feeding has advanced the start of breeding in other bird species (Kallander 1974, Smith et al. 1980, Ewald and Rohwer 1982, Davies and Lundberg 1985). It is clear, however, that differences did exist in the timing of pair formation between the two groups on different diet regimes.

The process of pair bond formation involves both sexes. The male must compete with other males through intense courtship for a mate while the female must choose the male exhibiting appropriate qualities. After the initial choice is made, pair compatibility and male quality is continually tested over an extended period, during which the bond can be dissolved or strengthened to the point where it becomes permanent (McKinney 1975, Williams 1983). A restricted diet will reduce the amount of energy and time each individual can commit to the pairing process. Male attentiveness during and after pairing may be an important cue used by the female (McKinney 1975), therefore low energy reserves may adversely affect this aspect of male quality. Conversely, the date of pairing and pair bond maintenance may not be influenced by male quality but by the female's physiological state. Diet restriction has been shown to influence hormone production which in turn can control reproduction (Akesson and Raveling 1981, Balthazart 1983, Bluhm 1985). Low body reserves may disrupt the physiological state of the female to a point at which pairing could be delayed or prevented. Once paired, the effects of food limitation on female physiological state may persist causing the female to abandon the male. Heitmeyer (1985) suggested that low body reserves in female mallards may alter their physiological state and delay or prevent the normal pairing process from taking place. This problem may also apply to males.

Early pairing in dabbling ducks may be a means by which individuals can test potential mates (McKinney 1975) but several authors have postulated that there are also direct advantages accrued by pairing early. An increase in dominance rank associated with the paired status has been documented for several waterfowl species (Raveling 1970, Paulus 1983, Hepp and Hair 1984, this study-Chapter 3). This increased status may facilitate access to limited resources (Ashcroft 1976, Scott 1980, Paulus 1983) and thereby allow the pair to acquire the energy reserves needed for both maintenance and reproduction (Hepp 1984). Early pairing would allow potential mates to strengthen pair bonds before strong bonds are required. Weak bonds may be ineffectual during periods of intense competition for resources, during challenges made by reproductively active males in winter, or during the establishment of breeding territories in the spring. Studies have shown that in some species, birds that have been paired for a longer period of time have a higher reproductive success than newly formed pairs (Mills 1973, Perrins and McCleery 1985).

Because forming and maintaining pair bonds entails costs in terms of time and energy, it would be advantageous to have high levels of energy reserves, and as discussed earlier, high energy reserves may be an indication of male quality. For both sexes, high levels of energy reserves may allow the pairing process to commence at an earlier date and thus enable a strong pair bond to form. Low energy reserves may disrupt and/or delay these critical biological processes. This could have a direct impact on the individual on the wintering grounds and ultimately affect its reproductive success the following spring.

Reproduction

Influence of pairing date

Several authors have suggested that, for ducks, the timing of pair bond formation can affect the date of laying indirectly by its influence on levels of body reserves during the winter period (Spurr and Milne 1976, Paulus 1983, Hepp 1984, Brodsky and Weatherhead 1985, Heitmeyer 1985). Because the pairing process is an important prelude to laying

(Akesson and Raveling 1981, Bluhm 1985), it is possible that pairing chronology may affect nesting chronology directly.

No correlation existed between pairing date and laying date in any of the four diet treatments, but several factors must be acknowledged before concluding that laying date has no relation to pairing date. This study, under captive conditions, removed some of the constraints to which mallards are subjected in their natural environment. First, early pairing did not appear to provide any advantage in the acquisition of energy reserves (Chapter 3), and second, these birds were not required to migrate or establish breeding territories. Because of the first condition the indirect advantages associated with early pairing did not exist. Because of the second, the relationship examined may have little relevance to the wild situation. Therefore, these results must be interpreted with caution and should not be used to refute the idea that there is either a direct or indirect influence of pairing chronology on nesting chronology.

Influence of body weight on laying

Both the level of body reserves and food resource abundance have been implicated as important determinants of laying date and clutch size in duck species that nest early in the breeding season (Krapu 1974, Krapu and Doty 1979, Drobney 1982, Coulson 1984, Duncan 1987). For the mallard it has been argued that energy reserves acquired before arrival on the breeding grounds allow the female to secure the necessary amount of protein during the post-arrival, pre-laying period for the egg production of her first clutch (Krapu 1981). Yet the relative importance of energy reserves acquired before arrival versus food abundance on the breeding grounds has never been quantified.

For captive mallards in this study, birds entering the breeding season with low body weights (minimal ene[illegible]ves) initiated clutches at a later date than those birds which had higher body weig[illegible]ut, there appeared to be no influence of body weight on clutch size when it was adjusted for laying date. In addition, low body weights before the start of the breeding season delayed clutch initiation significantly longer than did a restricted diet at the onset of the breeding season. These results support the suggestion that the level of endogenous reserves acquired before arriving on the breeding grounds can influence egg production in early nesting waterfowl. This point may be taken one step further. Environmental conditions south of the breeding grounds which affect the female's endogenous reserves may be a more important influence on clutch initiation dates than environmental conditions on the breeding grounds which affect food availability there. However, this interpretation is made with caution. The results are based on relative differences in the degree of restriction between the winter and spring periods. A change in the magnitude of the restriction during either period would probably have affected the magnitude of the observed differences in laying dates. For example, if the restriction during the winter period had been only 30% and the diet restriction during the spring period had been increased to 40% the observed results may have been reversed. Despite this possibility, the results show that endogenous reserves acquired prior to arrival on the breeding grounds can be more important to date of clutch initiation than environmental conditions on the breeding grounds which affect food availability.

To be of any biological significance a delay in laying date must decrease reproductive success of the individual. Duckling survival, a direct measure of reproductive success, is progressively reduced the later ducklings hatch in a species' breeding season (Dow and Fredga 1984, Hill 1984, Toft et al. 1984). Lower survival rates of later hatched young are also evident in other species of birds (Perrins 1970, Drent and Daan 1980, Cooke et al. 1984). A delay in laying date has also b[illegible] associated with decreased clutch size in many waterfowl species (Batt and Prince 1979, Davies and Cooke 1983, Hines and Mitchell 1983, Duncan 1987). Several proximate factors have been postulated to explain this correlation (Johnsgard 1973, Krapu et al. 1983) but laying date is probably the causal factor (see Duncan 1987). A smaller clutch size would decrease reproductive output of the individual for that breeding season. Finally, the number of nesting attempts may also be affected by a delay in the laying date. During the breeding season several constraints are placed on the female mallard (Titman 1981, Krapu 1981) and consequently, limitations of time and energy may dictate how many nesting attempts, and hence opportunities to produce young, can be made (Swanson et al. 1986). A delay in the initiation of the first nest may reduce the number of subsequent nesting attempts made by a female and this could ultimately reduce her reproductive output (Hegner and Wingfield 1986). Because early ground nesting ducks usually suffer high rates of nest loss (Balser et al. 1968), renests may provide a significant contribution to annual productivity (Higgins 1977).

Environmental conditions off the breeding grounds have been shown to influence reproductive output of birds on the breeding grounds (Jones and Ward 1976, Davies and Cooke 1983, Davies and Lundberg 1985). If the decision to breed is related to a threshold level of endogenous reserves, as has been suggested for several bird species (Ankney and MacInnes 1978, Boersma and Ryder 1983, Coulson 1984, Alisauskis and Ankney 1985) ,and these reserves are acquired prior to arrival on the breeding grounds, then one would expect to find two positive correlations. One between conditions off the breeding grounds and levels of endogenous reserves, and the second between conditions off the breeding grounds and recruitment rates the following year. Indeed, precipitation levels on the wintering grounds which are a good indicator of food abundance have been correlated with endogenous reserve levels in the mallard (Heitmeyer 1985) and pintail (Miller 1986) at the end of the winter period. As well, annual recruitment rates have been correlated with environmental conditions off the breeding grounds for the mallard (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987) and other species (Nilsson 1979, Den Held 1981, Davies and Cooke 1983).

To summarize, the results indicate that low body weights (low endogenous reserves) on arrival on the breeding grounds and reduced food availability after arrival will delay nest initiation but not affect clutch size. It also appears that laying date is affected more by low body weights on arrival on the breeding grounds than a restricted diet thereafter. The experimental design and methodology used in this captive study produced relative differences between treatment groups under an artificial situation, greatly simplifying the biological processes of a mallard relative to normal wild conditions. Nevertheless, I suggest that environmental conditions off the breeding grounds influence levels of endogenous reserves which in turn can affect laying dates, ultimately influencing reproductive output.

LITERATURE CITED

Afton, A.D. 1984. Influence of age and time on reproductive performance of female lesser scaup. Auk 101: 255-265.

Akesson, T.R., and D.G. Raveling. 1981. Endocrine and body weight changes of nesting and non-nesting Canada geese. Biol. Rep. 25: 792-804.

Alisauskas, R.T., and C.D. Ankney. 1985. Nutrient reserves and energetics of reproduction in American coots. Auk 102: 133-144.

Ankney, C.D., and C.D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95: 459-470.

Armbruster, J.S. 1982. Wood duck displays and pairing chronology. Auk 99: 116-122.

Ashcroft, R.E. 1976. A function of the pairbond in the common eider. Wildfowl 27: 101-105.

Balser, D.S., H.H. Dill, and H.K. Nelson. 1968. Effect of predator reduction on waterfowl nesting success. J. Wildl. Manage. 32: 669-682.

Balthazart, J. 1983. Hormonal correlates of behavior. Pp. 2[illegible]1-365. *in* Avian Biology, Vol. VII (D.S. Farner, J.R. King, and K.C. Parkes, Eds.). Academic Press, New York, New York.

Batt, B.D., and H.H. Prince. 1979. Laying dates, clutch size and egg weight of captive mallards. Condor 81: 35-41.

Bellrose, F.C. 1976. Ducks, Geese and Swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Bluh[illegible], C.K. 1985. Social factors regulating avian endocrinology and reproduction. Pp. 247-264 *in* The Endocrine System and the Environment (B.K. Follett, S. Ishii, and A. Chandola, Eds.). Japan Sci. Soc. Press, Tokyo, Japan/ Springer-Verlag, Berlin, West Germany.

Boersma, D., and J.P. Ryder. 1983. Reproductive performance and body condition of earlier and later nesting ring-billed gulls. J. Field Ornithol. 54: 374-380.

Brodsky, L.M., and P.J. Weatherhead. 1985. Time and energy constraints on courtship in wintering American black ducks. Condor 87: 33-36.

Cooke, F., C.S. Findlay, and R.F. Rockwell. 1984. Recruitment and timing of reproduction in lesser snow geese (*Chen caerulescens cairulescens*). Auk 101: 451-458.

Coulson, J.C. 1984. The population dynamics of the eider duck, *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. Ibis 126: 525-543.

Cowardin, L.M., D.S.Gilmer, and C.W. Shaffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildl. Monogr. 92.

Daly, M. 1978. The cost of mating. Am. Nat. 112: 771-774.

Davies, J.C., and F. Cooke. 1983. Annual nesting productivity in snow geese: prairie droughts and arctic springs. J. Wildl. Manage. 47: 291-296.

Davies, N.B., and A. Lundberg. 1985. The influence of food on time budgets and timing of breeding of the dunnock (*Prunella modularis*). Ibis 127: 100-110.

Den Held, J.J. 1981. Population changes in the purple heron in relation to drought in the wintering area. Ardea 69: 185-191.

Dixon, W.J., M.B. Brown, L. Engelman, J.W. Frane, M.A. Hill, R.I. Jennrich, and J.D. Toporek. 1983. BMDP Statistical Software. University of California Press, Berkeley, California.

Dow, H., and S. Fredga. 1984. Factors affecting reproductive output of the goldeneye duck, *Bucephala clangula*. J. Anim. Ecol. 53: 679-692.

Drent, R.H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Drobney, R.D. 1982. Body weight and composition changes and adaptions for breeding in wood ducks. Condor 84: 300-305.

Duncan, D.C. 1987. Nesting of northern pintails in Alberta: laying date, clutch size and renesting. Can. J. Zool. 65: 234-246.

Ewald, P.W., and S. Rohwer. 1982. Effects of supplemental feeding on timing of breeding, clutch size and polygyny in red-winged blackbirds, *Agelaius phoeniceus*. J. Anim. Ecol. 51: 429-450.

Farner, D.S., and B.K. Follett. 1979. Reproductive periodicity in birds. Pp. 829-872 *in* Hormones and Evolution, Vol. 2 (E.J.W. Barrington, Ed.). Academic Press, London, England.

Frankel, A. I., and T. S. Baskett. 1961. The effect of pairing on cooing of penned mourning doves. J. Wildl. Manage. 25: 372-384.

Fretwell, S.D. 1972. Populations in a Seasonal Environment. Princeton Univ. Press, Princeton, New Jersey.

Hegner, R.E., and J.C. Wingfield. 1986. Gonadal development during autumn and winter in house sparrows. Condor 88: 269-278.

Heitmeyer, M.E. 1985. Wintering strategies of female mallards related to dynamics of lowland hardwood wetlands in the Upper Mississippi Delta. Ph. D. Thesis, Univ. of Missouri, Columbia, Missouri.

Heitmeyer, M.E., and L.H. Fredrickson. 1981. Do wetland conditions in the Mississippi delta hardwoods influence mallard recruitment? Trans. North Am. Wildl. Nat. Resour. Conf. 46: 44-57.

Hepp, G.R. 1984. Dominance in wintering Anatinae: potential effects on clutch size and time of nesting. Wildfowl 35: 132-134.

Hepp, G.R. 1986. Effects of body weight and age on the time of pairing of American black ducks. Auk 103: 477-484.

Hepp, G.R., and J.D. Hair. 1983. Reproductive behavior and pairing chronology in wintering dabbling ducks. Wilson Bull. 95: 675-682.

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

Higgins, K.F. 1977. Ducks nesting in intensively farmed areas of North Dakota. J. Wildl. Manage. 41: 232-242.

Hill, D.A. 1984. Population regulation in the mallard (*Anas platyrhynchos*). J. Anim. Ecol, 53: 191-202.

Hines, J.E., and G.E. Mitchell. 1983. Gadwall nest-site selection and nest success. J. Wildl. Manage. 47: 1063-1071.

Johnsgard, P.A. 1960. A quantitative study of sexual behavior of mallards and black ducks. Wilson Bull. 72: 133-155.

Johnsgard, P.A. 1973. Proximate and ultimate determinants of clutch size in Anatidae. Wildfowl 24: 144-149.

Jones, P.J., and P. Ward. 1976. The level of reserve protein as the proximate factor controlling the time of breeding and clutch-size in the red-billed quelea (*Quelea quelea*). Ibis 118: 547-574.

Kallander, H. 1974. Advancement of laying of great tits by provision of food. Ibis 116: 365-367.

Kaminski, R.M., and E.A. Gluesing. 1987. Density and habitat related recruitment in mallards. J. Wildl. Manage. 51: 141-148.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4-85 *in* Avian Energetics (R.A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club. No. 15, Cambridge, Massachusetts.

Krapu, G.L. 1974. Feeding ecology of pintail hens during reproduction. Auk 91: 278-290.

Krapu, G.L. 1979. Nutrition of female dabbling ducks during reproduction. Pp. 59-70 *in* Waterfowl and Wetlands - An Integrated Review (T.A. Bookhout, Ed.). Proc. 1977 Symp., North Central Sect., The Wildl. Soc., Madison, Wisconsin.

Krapu, G.L. 1981 The role of nutrient reserves in mallard reproduction. Auk 98: 29-38.

Krapu, G.L., and H.A. Doty. 1979. Age-related aspects of mallard reproduction. Wildfowl 30: 35-39.

Krapu, G.L., A.T. Klett, and D.G. Jorde. 1983. The effect of variable spring water conditions on mallard reproduction. Auk 100: 689-698.

Lebret, T. 1961. The pair formation in the annual cycle of the mallard (*Anas platyrhynchos*). Ardea 49: 97-158.

McKinney, F. 1970. Displays of four species of blue-winged ducks. Living Bird 9: 29-64.

McKinney, F. 1975. The evaluation of duck displays. Pp. 331-357 *in* Function and Evolution in Behavior (G. Baerends, D. Beer, and A. Manning, Eds.). Clarendon Press, Oxford, England.

McLandress, M.R., and D.G. Raveling. 1981. Hyperphagia and social behavior of Canada geese, *Branta canadensis* prior to spring migration. Wilson Bull. 93: 310-324.

Miller, M. 1986. Northern pintail body condition during wet and dry winters in the Sacramento Valley, California. J. Wildl. Manage. 50: 189-198.

Mills, J.A. 1973. The influence of age and pair bond on the breeding biology of the red-billed gull, *Larus novaehollandiae scopulinus*. J. Anim. Ecol. 42: 147-162.

Milne, H. 1974. Breeding numbers and reproductive rate of eiders at the Sands of Forvie National Nature Reserve, Scotland. Ibis 116: 135-152.

Nilsson, L. 1979. Variation in the production of young swans wintering in Sweden. Wildfowl 30: 129-134.

Paulus, S.L. 1983. Dominance relations, resource use, and pairing chronology of gadwalls in winter. Auk 100: 947-952.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-265.

Perrins, C.M., and R.H. McCleery. 1985. The effect of age and pair bond on the breeding success of great tits, *Parus major*. Ibis 127: 306-315.

Raveling, D.G. 1970. Dominance relationships and agonistic behaviour of Canada geese in winter. Behaviour 37: 291-317.

SAS Institute Inc. 1985. SAS Introductory Guide, 3rd edition. Cary, North Carolina.

Scott, D.K. 1980. Functional aspects of the pair bond in winter in Bewick's swans (*Cygnus columbianus bewickii*). Beh. Ecol. Sociobiol. 7: 323-327.

Smith, J.N., 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.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. Freeman Co., San Francisco, California.

Spurr, E.B., and H. Milne. 1976. Factors affecting laying date in the common eider. Wildfowl 27: 107-109.

Sugden, L.G., and H.J. Poston. 1968. A nasal marker for ducks. J. Wildl. Manage. 32: 984-986.

Sugden, L.G., J. Thurlow, R.D. Harris, and K. Vermeer. 1974. Investigations of mallards overwintering at Calgary, Alberta. Can. Field-Nat. 88: 303-311.

Swanson, G.A., T.L. Shaffer, J.F. Wolf, and F.B. Lee. 1986. Renesting characteristics of captive mallards on experimental ponds. J. Wildl. Manage. 50: 32-38.

Titman, R.D. 1981. A time-activity budget for breeding mallards (*Anas platyrhynchos*) in Manitoba. Can. Field-Nat. 95: 266-271.

Toft, D.A., D.L. Trauger, and H.W. Murdy. 1984. Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Athya*, Anatidae) and a proposed evolutionary explanation. J. Anim. Ecol. 53: 75-92.

Turnbull, R. E., and G. A. Baldasarre. 1987. Activity budgets of mallards and American Wigeon wintering in east-central Alabama. Wilson Bull. 99: 457-464.

Weller, M. W. 1965 Chronology of pair formation in some nearctic Athya (Anatidae). Auk 82: 227-235.

Williams, B.K., and J.D. Nichols. 1984. Optimal timing in biological processes. Amer. Nat. 123: 1-19.

Williams, D.M. 1983. Mate choice in the mallard. Pp. 297-309 *in* Mate Choice (P. Bateson, Ed.). Cambridge University Press, New York, New York.

Wishart, R.A. 1983a. The behavioural ecology of the American wigeon (*Anas americana*) over its annual cycle. Ph. D. thesis, University of Manitoba, Winnipeg, Manitoba.

Wishart, R.A. 1983b. Pairing chronology and mate selection in the American wigeon (*Anas americana*). Can. J. Zool.: 1733-1743.

V. CONCLUDING DISCUSSION

This study documented differential female emigration from a population of wild mallards (*Anas platyrhynchos*), wintering at the latitude of Edmonton, and using captive ducks, investigated the importance of dominance behaviour and body reserves to the well-being of the individual. I also attempted to clarify the importance of dominance status and body reserves of mallards during the winter period on their subsequent reproductive success.

Observations of wild mallards wintering north of their normal range indicated that the sex ratio was heavily biased towards males and that this bias was created at the onset of winter (freeze-up of river). The proportion of females and the size of the population also gradually declined during one winter in which environmental conditions were extremely harsh. Because this population is subjected to environmental conditions far more severe than populations located at more southerly latitudes, I suggest that differential dispersal at the onset of winter is more important in changing the sex ratio than differential mortality rates. However, the proximal mechanism(s) causing this differential dispersal is (are) still unclear. Exclusion (Gauthreaux 1978) based on the dominant-subordinate relationship of males and females (Hepp and Hair 1984, Alexander 1987) at a time when both space and food availability are drastically reduced, may induce the subordinate females to emigrate in greater numbers than males. The ultimate cause may be a means of avoiding mortality induced by a negative thermal balance (Calder 1974) or, possibly due to exclusion. As well, it may be important for females to avoid low body reserves which could reduce reproductive output (Hepp 1984), even if it does not kill them (Brodsky and Weatherhead 1985).

A dominant-subordinate relationship was observed in the captive mallards as has been described for wild duck populations (Paulus 1983, Hepp and Hair 1984). Males dominated females and paired birds dominated single birds of both sexes. Within sex comparisons indicate that neither body size nor weight, nor experience as a sibling had significant effects on adult status. However, age (within a year class) influenced the dominance status achieved by females. Aggressive interactions occurred at very low rates in this study, as has been observed in wild populations (Paulus 1980, Hepp and Hair 1984), yet distinct dominance classes existed. These relationships appeared to be established with little overt aggression, yet of the variables measured that could be used to signal dominance status, none was correlated with dominance status. I suggest that subtle behavioural cues such as posture are used to establish dominance relationships and that these cues are mediated by hormone levels. Age and pair status are two factors which affect hormone production (Akesson and Raveling 1981) and both are related to dominance status in these ducks.

Resource limitation caused an increase in the number of agonistic interactions observed. If exclusion was the proximate mechanism prompting differential female dispersal at the onset of winter then increased interaction rates should also be observed at this time in populations of wild mallards. To date, this phenomenon has not been documented. The absence of agonistic interactions over resources which were abundant gives some support to the suggestion that aggressive interactions recorded in wild populations of ducks, do represent competition for limited resources.

The ability to acquire limited resources appears to be related to dominance status. In an environment where the number of females were reduced, dominant males paired earlier and possibly more often than subordinates, thereby enhancing their chances of reproducing (Wishart 1983). Dominants (paired males) also used preferred loafing locations more frequently than subordinates, an advantage that would probably reduce the likelihood of predation (Hamilton 1971). Dominance status (sex) did not appear to affect levels of lipid reserves through priority of access to limited food resources. These results are in contrast to those found for corvid (Craig et al. 1982) and other passerine species (Fretwell 1969, DeLaet 1985). Thus inferences made about the advantages of dominance status in waterfowl (Paulus 1983, Hepp 1984, Alexander 1987) regarding acquisition of critical, limited food resources were not confirmed. Nevertheless, within each sex dominance status was positively correlated with lipid reserves. Because the results of this study may have been influenced by the experimental design, I suggest that more work is needed before definitive conclusions can be reached.

Low body weight, an indication of reduced body reserves, delayed initiation of courtship and pairing , and decreased the number of permanent pair bonds formed. This suggests that there exists an important relationship between body reserves prior to arrival on the spring breeding grounds (during winter period) and reproductive activity. To be detrimental, a delay in the pairing process must adversely affect the individual or its ability to produce young. For the male, any delay may prevent mate acquisition because females are a limited resource (Wishart 1983). Because single females are subordinate any delay in pairing may hamper their acquisition of critical food resources (Paulus 1983). In addition, unstable pair bonds resulting from poor condition may hamper the male's ability to protect its mate from sexual advances by other males (Wishart 1983). Low body weight during the winter period delayed nesting to a greater degree than reduced body weight during the spring period in this study of captive mallards. Delayed nesting may decrease reproductive output by decreasing clutch size (Duncan 1987), by reducing the number of renesting attempts made (Hegner and Wingfield 1986), and by decreasing the survival of ducklings hatched later in the species' breeding season (Toft et al. 1984). Thus, if a female arrived on the breeding grounds with low body reserves relative to other females, her reproductive output in that year would probably be reduced.

The biological significance of dominance status and body reserves during the winter period is a topic which has generated much interest in recent years among waterfowl biologists. Variable climatic conditions have been correlated with levels of body reserves (Heitmeyer 1985, Miller 1986) and dominance status has been associated with access to critical resources (Paulus 1983, Alexander 1987). A correlation also exists between climatic conditions on the wintering grounds and reproductive output the following year (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987). This study of captive mallards demonstrated that individuals differ in their dominance status which in turn can influence, to some degree, an individual's well-being. However, the critical question as to whether dominance status can influence levels of body reserve threw priority of access to limited food resources, was not answered.

Interpretation of these results must be tempered with caution. First, the captive environment introduced the possible bias of individual recognition during aggressive interactions which is unlikely to occur in the wild (Raveling 1970). Second, artificial feeding removed the rigours of the natural environment providing ample time for investing in other activities such as courtship. And finally, spring migration and breeding territory establishment were two important activities omitted from the biological cycle of these mallards. This simplified the relationship between winter conditions and spring reproduction of these birds. Yet, despite these simplifications, during the winter period, it is apparent that both social and environmental factors have an important influence on the well-being of mallards.

LITERATURE CITED

Akesson, T.R., and D.G. Raveling. 1981. Endocrine and body weight changes of nesting and non-nesting Canada geese. Biol. Rep. 25: 792-105.

Alexander, W.C. 1987. Aggressive behavior of wintering diving ducks (*Aythyini*). Wilson Bull. 99: 38-49.

Brodsky, L.M., and P.J. Weatherhead. 1985. Time and energy constraints on courtship in wintering American black ducks. Condor 87: 33-36.

Calder, W.A. 1974. Consequences of body size for avian energetics. Pp. 86-144 *in* Avian Energetics (R.A. Paynter, Ed.). Nuttal Ornithol. Club Publ. No. 15, Cambridge, Massachusetts.

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

DeLaet, J.F. 1985. Dominance and anti-predator behaviour of great tits *Parus major*: a field study. Ibis 127:372-377.

Fretwell, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Juncos hyemalis*). Bird-banding 40: 1-23.

Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. Pp. 17-54 *in* Perspectives in Ethology, Vol.3 (P.P.G. Bateson, and P.H. Klapfer, Eds.). Plenum Press, New York, New York.

Hamilton, W.D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31: 295-311.

Hegner, R.E., and J.C. Wingfield. 1986. Gonadal development during autumn and winter in house sparrows. Condor 88: 269-278.

Heitmeyer, M.E. 1985. Wintering strategies of female mallards related to dynamics of lowland hardwood wetlands in the upper Mississippi delta. Ph.D. thesis, University of Missouri, Columbia, Missouri.

Heitmeyer, M.E., and L.H. Fredrickson. 1981. Do wetland conditions in the Mississippi delta hardwoods influence recruitment? Trans. North Am. Wildl. Nat. Resour. Conf. 46: 44-57.

Hepp, G.R. 1984. Dominance in wintering Anatinae: potential effects on clutch size and time of nesting. Wildfowl 35: 132-134.

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

Kaminski, R.M., and E.A. Gluesing. 1987. Density- and habitat-related recruitment in mallards. J. Wildl. Manage. 51: 141-148.

Miller, M. 1986. Northern pintail body condition during wet and dry winters in the Sacramento Valley, California. J. Wildl. Manage. 50: 189-198.

Paulus, S.L. 1980. The winter ecology of the gadwall in Louisiana. M.S. thesis, University of North Dakota, Grand Forks, North Dakota.

Paulus, S.L. 1983. Dominance relationships, resource use, and pairing chronology of gadwalls in winter. Auk 100: 947-952.

Raveling, D.G. 1970. Dominance relationships and agonistic behaviour of Canada geese in winter. Behaviour 37: 291-317.

Toft, D.A., D.L. Trauger, and H.W. Murdy. 1984. Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Athya*, Anatidae) and a proposed evolutionary explanation. J. Anim. Ecol.53: 75-92.

Wishart, R.A. 1983. Pairing chronology and mate selection in the American wigeon (*Anas americana*). Can. J. Zool. : 1733-1743.