THE UNIVERSITY OF MANITOBA

PINTAIL BROOD HEN BEHAVIOUR:
PATTERNS OF PARENTAL INVESTMENT

by

SHIRLEY JANE RUSHFORTH

A THESIS

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ABSTRACT

Parental time investment by Pintail (Anas acuta) brood hens was studied at Oak Hammock Marsh, Manitoba during the summer of 1979. Behaviours directly related to brood care and maintenance of the hens' physical condition were combined to form a parental investment and self maintenance category respectively. The data were analyzed with respect to brood size, brood age and time of year.

Approximately 50% of the hens' time (during observation periods) was spent feeding. Subsurface feeding was more commonly used to obtain food than was surface feeding. Hens spent more time investing in themselves than in the brood. Monitoring brood position was the most time consuming component of parental investment.

Hens with small broods spent more time subsurface feeding than hens with larger broods. Brood size had no effect on the remaining behaviours or on parental investment and self maintenance.

Hens spent more time surface feeding with downy young than with feathered young and more time subsurface feeding with feathered young than with downy young. More time was involved in leading young to safety, to feeding sites and to loafing sites when they were downy than when feathered. Hens used "swim behind" to monitor the position of downy young and "low alert" to monitor the position of feathered young. Brood age had no effect on parental investment or on self maintenance.

Subsurface feeding increased significantly over the season while surface feeding fluctuated. Feeding increased from approximately 36% of the hens' time in mid to late June to 69% in early to mid-August. Hens spent less time leading young to safety, to feeding sites and to loafing sites as the season advanced. Time spent monitoring brood position was high in late June and decreased in mid-August. Parental investment decreased significantly over the summer while self maintenance increased.

Aspects of inter- and intraspecific brood defence were described. Pintail brood hens initiated 94% of the interactions observed. The majority of these interactions involved other Pintails, the second highest number involved American Coots (*Fulica americana*) and the third highest involved Mallards (*Anas platyrhynchos*). Ninety percent of interactions initiated by Pintail brood hens resulted in victory for the brood hen.

ACKNOWLEDGEMENTS

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES cont'd.

LIST OF APPENDICES

INTRODUCTION

Trivers (1972) defined parental investment as any investment by the parent in an individual offspring (such as guarding or feeding the young) that increases the probability of the offspring surviving, at the cost of the parent's ability to invest in other offspring. Several theories regarding parental investment have been proposed. An evolutionary model developed by Trivers (1974) predicts that parental investment should begin to decline at a point when the cost of investment by the parent is greater than the benefit to the young. A decline in investment at some critical stage in offspring development has been reported for Rhesus Macaques (*Maca mulatta*) (Hinde and Spencer-Booth 1971), Mountain Bighorn Sheep (*Ovis canadensis*) (Berger 1979), White Pelicans (*Pelecanus erythrorhynchos*) (Schaller 1964), Eastern Kingbirds (*Tyrannus tyrannus*) (Morehouse and Brewer 1968), Red Warblers (*Ergaticus ruber*) (Elliot 1969) and Pink-footed Geese (*Anser brachyrhynchus*) (Lazarus and Inglis 1978).

A second theory predicts that larger broods will require greater parental investment than smaller broods (Walsberg 1978). Smith (1978), Haftorn (1978), Lazarus and Inglis (1978), Walsberg (1978), Robertson and Biermann (1979) and Biermann (1980) have discussed the effects of brood size on parental investment.

With the exception of Lazarus and Inglis' (1978) work on Pink-footed Geese, Trivers' theory has only been tested in species that feed their young and the effect of brood size on parental investment has only been tested in altricial species. Work testing these two theories has also involved only those species where both sexes participate in parental care. Thus it is of interest to examine parental time investment in a precocial species where no parental feeding occurs and only one parent cares for the young. The Pintail (*Anas acuta*) was chosen for study because it exhibits these characteristics and a large number of individuals could easily be observed on the study area.

Thus two objectives of this study were 1) to determine if parental investment will decline at some point when the hen is with the brood and 2) to determine if parental investment is affected by brood size.

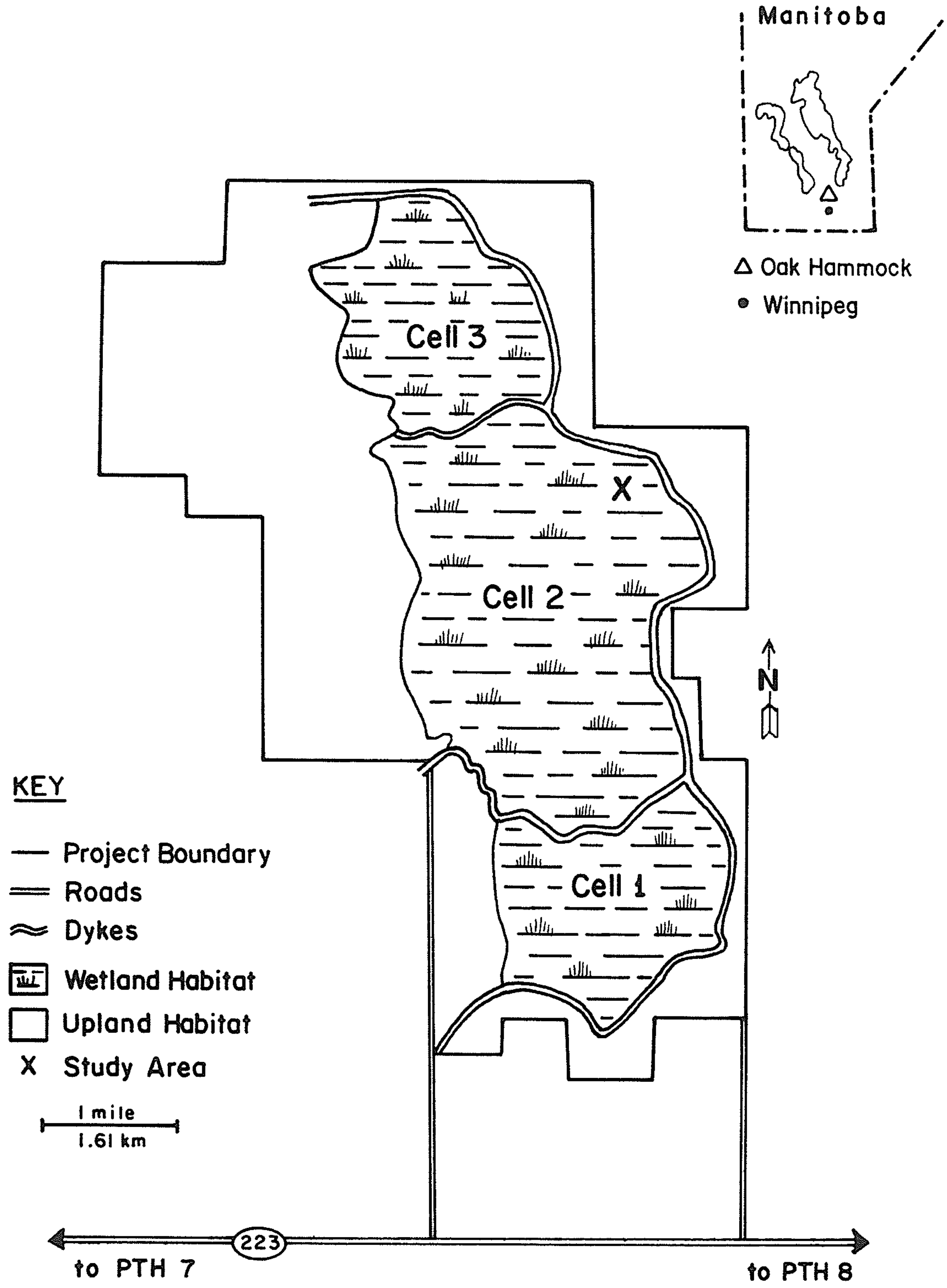
Ducks are known to renest after losing a clutch (Keith 1961; Gates 1962) or a brood (Sowls 1949) and occasionally after successfully hatching a brood (Rogers and Hanson 1967; Titman and Lowther 1975). Consequently duckling hatching dates are spread over several months and the rearing of late broods may coincide with molt or deposition of premigratory fat. Reproduction, molt and deposition of premigratory fat are thought to be incompatible activities (Kendeigh 1949; Payne 1972) since they require energy above that needed for existence. Thus I also tested the hypothesis that parental investment in Pintails may vary with time of year.

STUDY AREA AND METHODS

The study was carried out at Oak Hammock Marsh Wildlife Management Area (for a description of the marsh see Oetting and Dixon 1975) which is located in southern Manitoba (latitude $51^{\circ}7.5'$N, longitude $97^{\circ}40'$W). The study site was situated in the northeast corner of the middle cell (Fig. 1) where Pintail brood hens and broods were most abundant and lack of dense vegetation facilitated observation.

Time budget data for females with broods were collected 6 days each week from 16 June 1979 when broods were first observed using the marsh, to 15 August 1979 when adults began flocking. A schedule was arranged such that the periods from 05:00 to 13:00 hours and 13:00 to 21:30 hours were each sampled 3 times per week. Rain, preventing entrance to the marsh, and lack of visible broods reduced the potential number of research hours. Observations were made from a car on the dyke using a 20-60X zoom spotting scope and 7X35 binoculars. Behaviours were recorded on data sheets at 15 second intervals using a metronome timing device (Wiens *et al*. 1970). I attempted to obtain 30 minutes of continuous records on each hen observed.

Figure 1. Oak Hammock Marsh Wildlife Management Area, Manitoba.


Manitoba
Oak Hammock
Winnipeg
Cell 3
Cell 2
Cell 1
X
N
KEY
Project Boundary
Roads
Dykes
Wetland Habitat
Upland Habitat
X Study Area
1 mile
1.61 km
223
to PTH 7
to PTH 8

Date, time of day, brood age and brood size were recorded for each set of time budget data. Ducklings were aged according to plumage classes (Gollop and Marshall 1954). Class I are down covered, first feathers appear in class II and class III ducklings are fully feathered but incapable of flight. Data on hens with class III young were not collected as I was unable to distinguish them accurately from adults or young of the year already capable of flight. Mixing of broods was never observed and therefore brood sizes are assumed to be accurate.

Brood hens were chosen for observation by scanning the study area and time-budgeting the hen of the first brood located, usually within 200 meters from me. In order to reduce the chance of obtaining more than one set of data on the same hen, broods corresponding in size and age to those already time-budgeted in one day were ignored, unless there was evidence that 2 or more such broods existed.

Dyke edges and islands were used by Pintails for loafing and in most cases, broods that used these areas were obscured from view by other birds or by dense vegetation. This fact and the scanning technique used may have biased the data towards behaviours occurring on the water. Therefore an attempt was made to time budget one brood per week, as long as possible, in order to obtain some information on total daily cycles.

All behaviours were included in the time budget. Since some were rarely observed, they were eliminated from analysis. Those included in the analysis were defined as follows:

Low Alert (LA) - hen assumed a head upright posture and was not engaged in other activities (after Lazarus and Inglis 1978).

High Alert (HA) - hen assumed a head upright posture with neck extended and was not engaged in other activities. This behaviour usually occurred as a result of a disturbance (after Lazarus and Inglis 1978).

(At the beginning of the field season, I did not differentiate between HA and LA, but recorded them cumulatively as alert. It became obvious that they were two separate behaviours and I began recording them as such. Consequently sample sizes for these two categories are lower than for the remainder.)

Swim Lead (SL) - hen was distinctly leading the brood in some particular direction, usually with more than one half of the brood behind her.

Swim behind (SB) - hen was distinctly following the brood, usually with more than one half of the brood in front.

Comfort Movements (CM) - included all activities related to body maintenance, such as preening and bathing (Dwyer 1975).

Feed (FE) - Involved the action of obtaining food. Relocating during feeding was classified as locomotion (Dwyer 1975).

Ducks utilize several different methods of obtaining food from the water. These can be categorized as surface and subsurface feeding. Surface feeding permits the hen to feed and watch the brood simultaneously, as her eyes are above the marsh surface, while subsurface feeding obstructs the hen's view of the brood. Hens that obtain food from the surface more often than from the subsurface of the marsh, would have more time available for monitoring brood position. Thus surface and subsurface feeding were recorded during the time budget and defined as follows:

Surface (SUR) - hen submerged all or part of the bill into the water.

Subsurface (SUB) - hen submerged entire head or hen submerged head and neck into the water.

Pintail brood hens and their broods interacted with other birds on the study area. Since these interactions were infrequent in occurrence, they were recorded opportunisitically during each observation period. Interactions consisted of three intensities:

Threat - open bill postures directed towards another bird.

Pursuit - chasing or swimming toward another bird, often with bill open.

Attack - involved pecking or fighting with another bird.

All intensities of interactions involved both inter- and intraspecific interactions. The aggressor, victim and winner were recorded for interactions whenever possible.

Parental feeding of the young is frequently used as a measure of parental investment. While parental feeding does not occur in Pintails, females remain with the young approximately until they are fully feathered, indicating some investment. Observations made during this study indicated that parental investment by Pintail hens was accomplished by the following behaviours: low alert, high alert, swim lead and swim behind. Different functions have been described for these behaviours. Swim behind and low alert function in monitoring the position of the brood to prevent straying of highly mobile young (Beard 1964). High alert functions in watching for predators (Lazarus and Inglis 1978) and swim lead functions in leading the young to safety, to feeding sites and to loafing sites (Beard 1964). Personal observations suggested that the parental investment behaviours used by Pintails functioned as described above. These behaviours often showed opposing trends (e.g., swim behind decreased with brood age while low alert increased). In order to test parental investment theory, a parental investment category (including swim lead, swim behind, low alert, high alert) and a self maintenance category (including feed and comfort movements) were formed. Behaviours classified as parental investment may benefit the hen. Similarly, behaviours classified as self maintenance will benefit the brood, since a hen in good condition will have more energy to invest in the brood than a hen in poor condition. For analytical purposes, parental investment and self maintenance were assumed to be mutually exclusive categories.

STATISTICAL ANALYSIS

Time spent at each behaviour (including surface and subsurface feeding) was converted to the percent time spent at total activities for all data sets with 20 to 30 minutes of continuous observation. Each of these data sets corresponds to 1 sample unit. All usable data sets were assumed to be independent. Data were analyzed using the BMDP-P series (Biomedical Computer Programs) statistical package (Engleman *et al*. 1979). Time of year and brood age were coded for the analysis.

Multivariate analysis of covariance was used to determine if brood size, brood age and time of year (X variables) affected the percent time spent at the categorized behaviours and at parental investment and self maintenance (Appendix C.14; Engleman *et al*. 1979). Three analyses were performed: 1) with LA, HA, SL, SB, FE and CM as the Y variables, 2) with FE replaced by surface and subsurface feeding, and 3) with parental investment and self maintenance as the Y variables.

The X variables were not significantly correlated (R^2 = 0.17 for brood age and time of year, R^2 = 0.18 for brood size and time of year and R^2 = 0.02 for brood size and brood age), thus it was possible to use them as treatments or covariates. When brood size was the treatment, brood age and time of year were used as covariates. When brood age was the treatment, brood size and time of year were used as covariates, and when time of year was the treatment brood age and brood size were used as covariates. Consequently when a particular X was the treatment, the confounding effects of the other two X variables were removed.

The problem of singularity can be encountered when using percent data in multivariate analysis. This was avoided by the elimination of infrequently occurring behaviours from each data set.

Assumptions of univariate data were tested, since the program used initially performs an analysis of variance on all factors. Percent data often require an arcsine transformation to draw out the tails into a normal curve (Sokal and Rolf 1969). Data from this study did not require this transformation. Independence of the variance from the mean was tested using regression analysis. Groups not conforming to this assumption were transformed by use of ln (x + 1) transformation as indicated by Taylor's Power Law. After transformations were performed, Levine's test indicated that variances were not significantly different.

When significant differences were obtained from the multivariate analysis of covariance, the Least Significant Difference Method of multiple comparisons (Snedecor and Cochran 1967) was used. Means and 95% confidence intervals were presented graphically.

Where insufficient data and method of collection prevented statistical analysis, descriptive techniques were employed.

RESULTS AND DISCUSSION

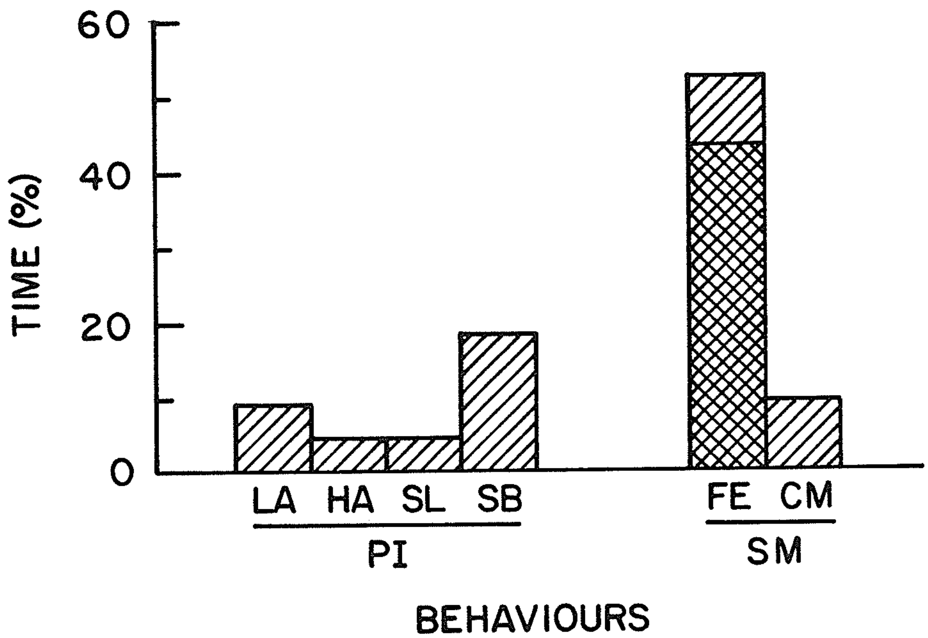
General Behaviour

Pintail brood hens spent more time investing in themselves (60.8%) than in their broods (35.5%) (Fig. 2). This is consistent with an evolutionary trend described for waterfowl (Kear 1970). Minimal parental care is associated with the production of large broods (ducks), while "lavish" parental care is associated with the production of small broods (swans).

Brood hens spent more time feeding (51.9 $\pm$ 20.2 S.D.) during the brood rearing season than at any other behaviour. Subsurface feeding (43.3 $\pm$ 23.3) was more commonly used to obtain food than was surface feeding (8.5 $\pm$ 11.9). Krapu (1974) also found that subsurface feeding was the most common method by which Pintails obtained food. Time spent swimming behind (18.2 $\pm$ 13.7) was greater than that spent at the remaining behaviours and was the most time consuming component of parental investment. On average comfort movements (8.9 $\pm$10.4) and low alert (8.9 $\pm$6.8) involved more time than swim leading (4.3 $\pm$ 8.5) and high alert (4.1 $\pm$ 4.7).

The prevalence of feeding during the brood rearing season has been described for a variety of other waterfowl species. Grazing was one of the most frequent activities in the Pink-footed Goose and was allocated similar amounts

Figure 2. Mean percent time spent at each behaviour by Pintail brood hens. The cross hatching on the feed bar represents the percent time spent subsurface feeding while the remainder of the bar represents the percent time spent surface feeding. N = 193 for SL, SB and CM. N = 130 for LA and HA. (Henceforth LA = low alert, HA = high alert, SL = swim lead, SB = swim behind, FE = feed, CM = comfort movements, PI = parental investment and SM = self maintenance.


60
40
20
0
TIME (%)
LA
HA
SL
SB
PI
FE
CM
SM
BEHAVIOURS

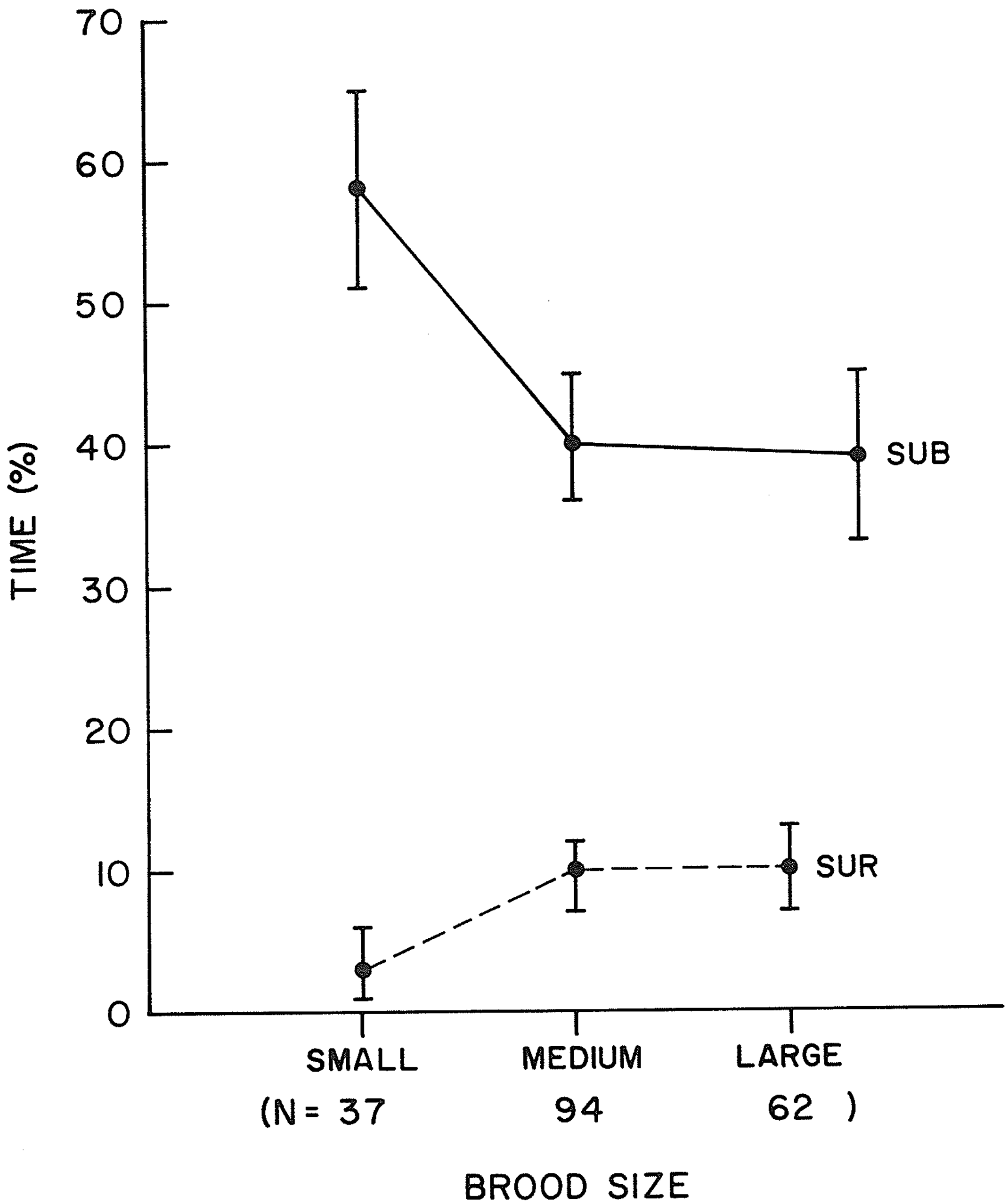
of time by parents and non-parents (Lazarus and Inglis 1978). Maccoa Duck (*Oxyura maccoa*) brood hens spent 50% of each day (dawn to dusk) feeding (Siegfried *et al*. 1976) while female Cackling Geese (*Branta canadensis minima*) fed nearly constantly with their broods (Raveling 1979).

In ducks, the peak energetic expense of reproduction occurs prior to the brood rearing season (Case 1978). This expense may cause the hen's condition to deteriorate (Harris 1970). Hens have been reported to undergo a progressive decrease in weight during incubation (Fuller 1953; Krapu 1974). Fifty percent of this loss is due to involution of ovary and oviduct, while the remaining 50% is due to loss of metabolic reserves (Harris 1970). Thus it was necessary for hens to spend a large proportion of their time feeding in order to restore body weight, and provide energy for brood rearing and for molt and migration later in the season.

Brood Size

Brood sizes were classified as small, medium and large containing 1 to 3, 4 to 6, and 7 to 9 young respectively. Time spent subsurface feeding varied significantly with brood size ($F = 3.857$; d.f. = 2 and 187; $P < 0.05$). Hens with small broods spent more time subsurface feeding ($P < 0.001$) than hens with medium or large broods (Fig. 3). Time spent

Figure 3. The effect of brood size on the percent time Pintail brood hens spent surface (SUR) and subsurface (SUB) feeding.



TIME (%)
70
60
50
40
30
20
10
0
SUB
SUR
SMALL
MEDIUM
LARGE
(N= 37
94
62)
BROOD SIZE

surface feeding was not significantly affected by brood size ($P > 0.05$), although there was a trend for hens with small broods to spend less time surface feeding than hens with larger broods.

In altricial birds where young depend on their parents mainly for food, an increase in brood size results in an increase in feeding rates (Moreau 1947; Skutch 1967; Lack 1973; Haftorn 1978; Walsberg 1978; Robertson and Biermann 1979). In Pintails where the young depend on the female mainly for protection from predators and maintenance of brood unity, an increase in brood size appears to correspond with increased monitoring of brood position. This investment is accomplished by increasing time spent surface feeding, rather than replacing feeding with brood monitoring behaviours.

Differential investment between large and smaller broods may be related to brood structure and behaviour. Large broods tended to be spaced over a greater area, with some ducklings being farther from the hen than in a similarly spaced small brood. Since ducklings were observed to disperse when feeding, rather than remaining in a cohesive unit, each duckling required individual monitoring. Thus large broods required more attention than smaller ones. Large broods may deplete localized food supplies faster than small broods, making it necessary for the brood to relocate more frequently during feeding. Hens subsurface feeding would tend to get left behind to a greater extent than those bill-dipping or dabbling on the surface. Casual observations suggested that this was true.

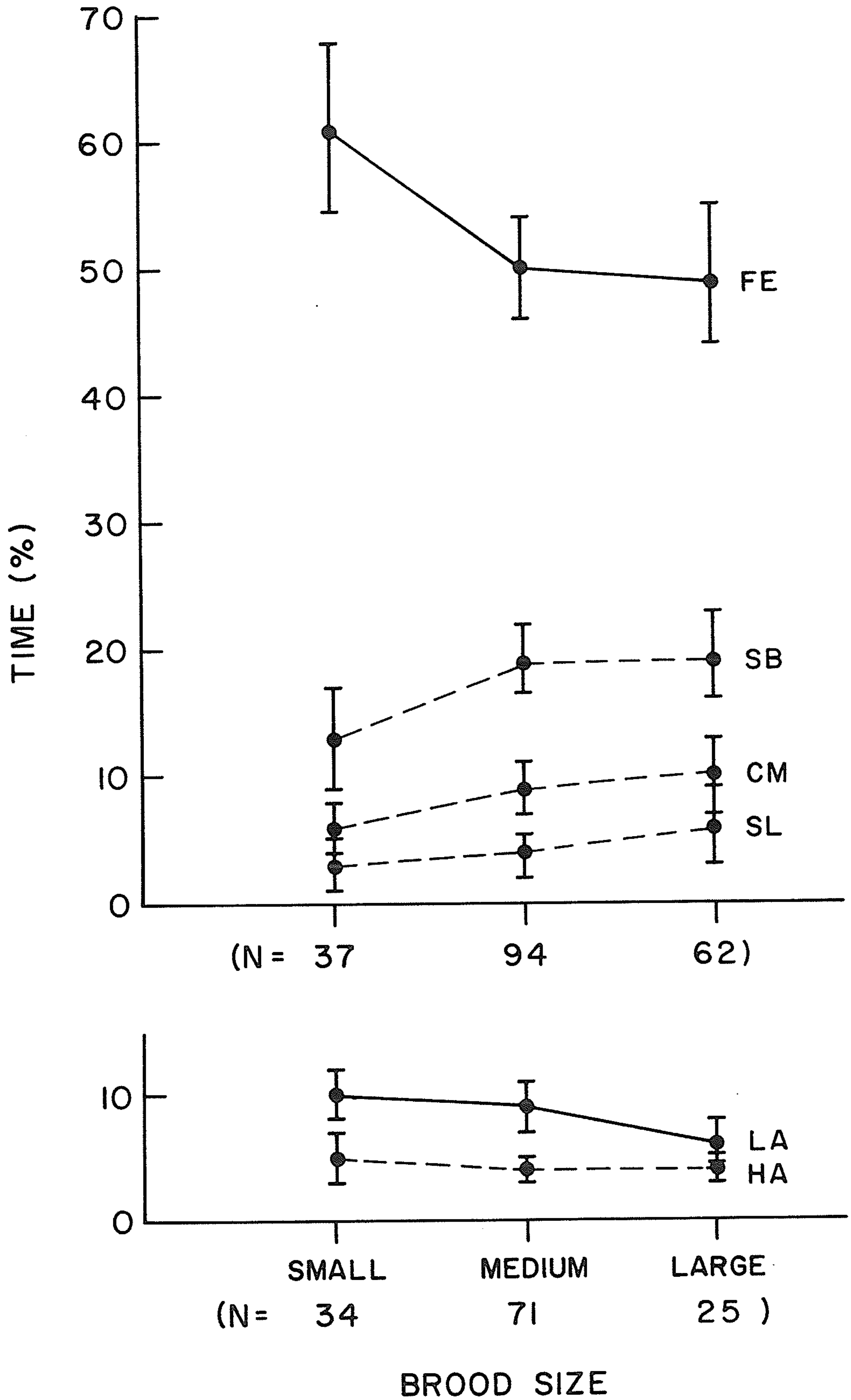
Lazarus and Inglis (1978) found no effect of brood size on parental behaviour of the Pink-footed Goose. Unlike ducks, male geese contribute to parental care by guarding the brood while the female feeds (Lazarus and Inglis 1978). Thus goslings are under constant surveillance and differences in brood size may be less important than in ducks.

Brood size also had no significant effect on the remaining Pintail brood hen behaviours, although hens with small broods appeared to spend more time feeding and less time swimming behind than hens with medium and large broods (Fig. 4). Brood size had no significant effect on parental investment or self maintenance. However there was a tendency for parental investment to increase and self maintenance to decrease between small and larger broods (Fig. 5).

Brood Age

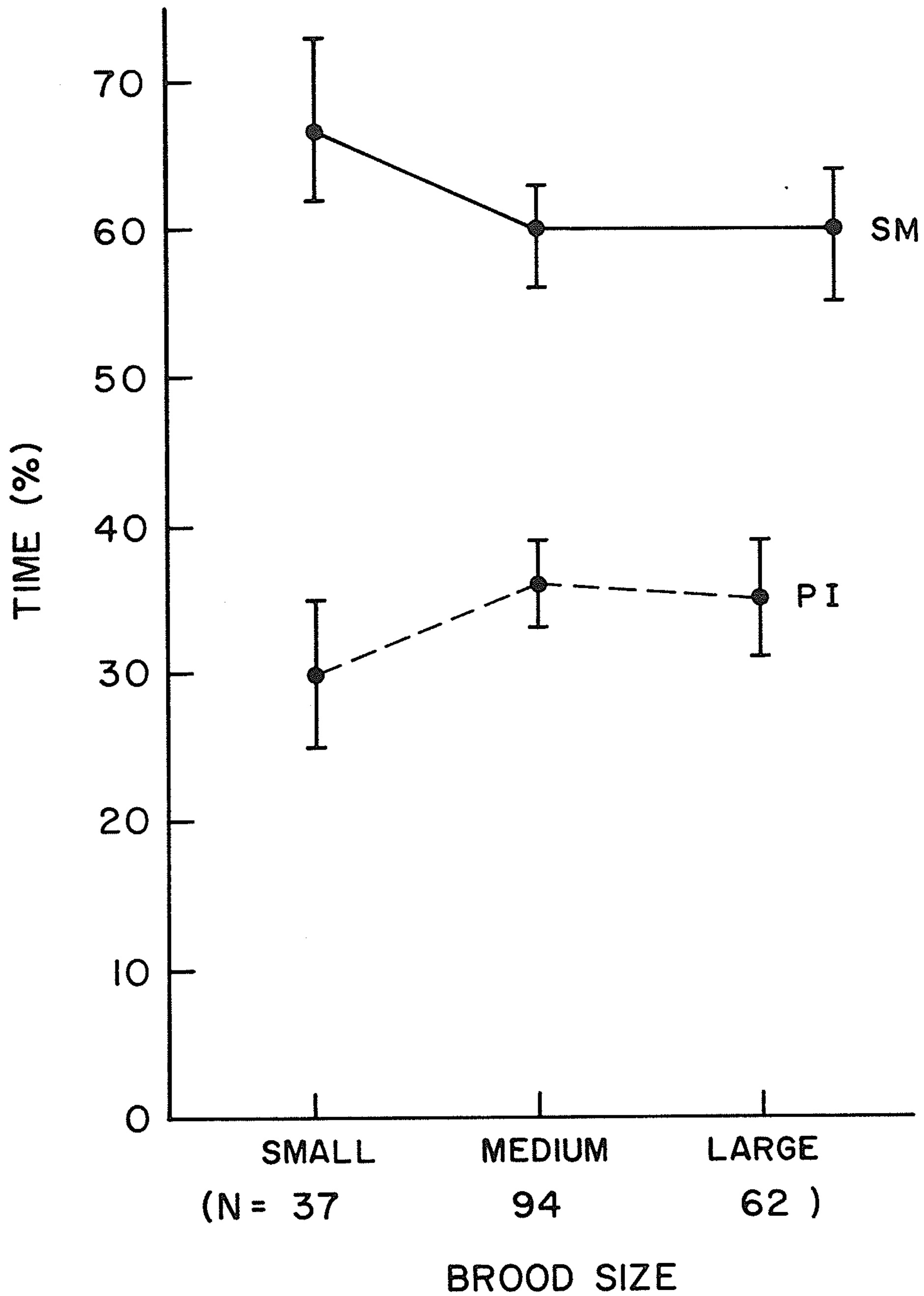
Surface ($F = 10.221$; d.f. = 1 and 188; $P < 0.01$) and subsurface feeding ($F = 3.882$; d.f. = 1 and 188; $P < 0.05$) varied significantly with brood age (Fig. 6). Brood hens

Figure 4. The effect of brood size on the percent time Pintail brood hens devoted to different behaviours.



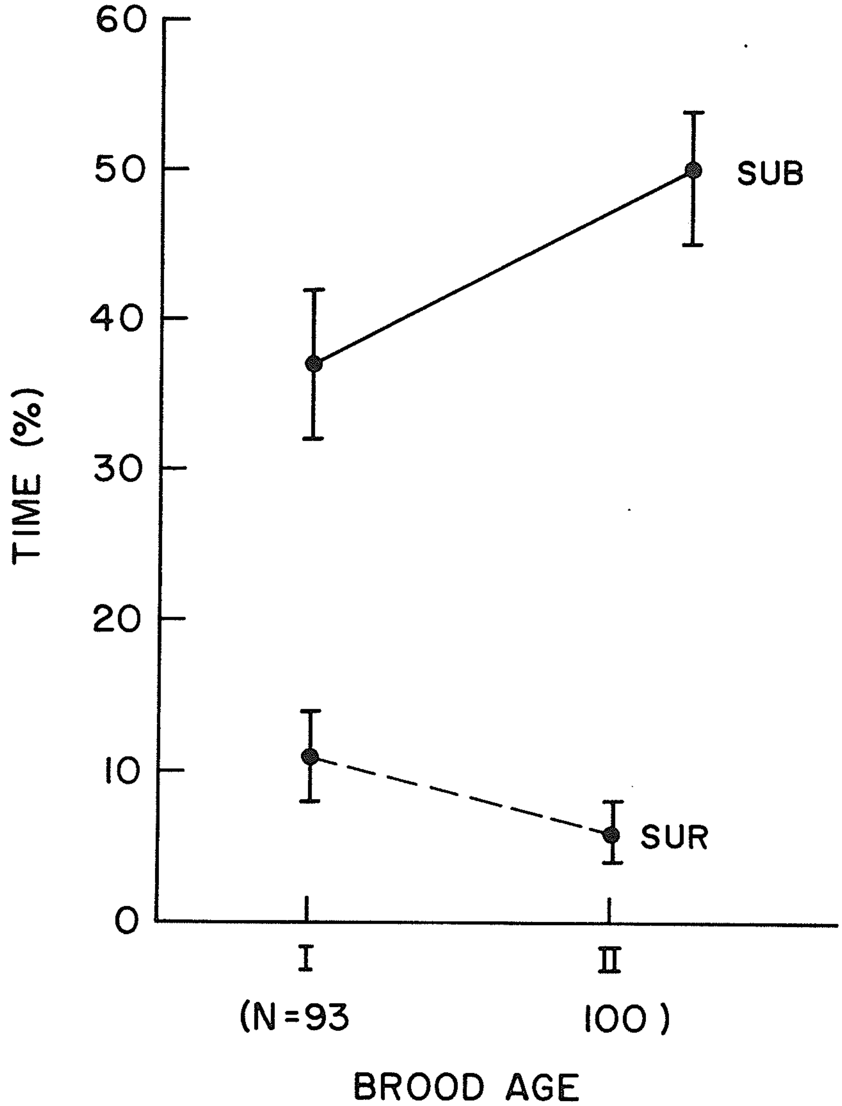
70
60
50
40
30
20
10
0
TIME (%)
FE
SB
CM
SL
(N= 37
94
62)
10
0
LA
HA
SMALL
MEDIUM
LARGE
(N= 34
71
25)
BROOD SIZE

Figure 5. The effect of brood size on parental investment (PI) and self maintenance (SM) by Pintail brood hens.



TIME (%)
70
60
50
40
30
20
10
0
SM
PI
SMALL
MEDIUM
LARGE
(N= 37
94
62)
BROOD SIZE

Figure 6. The effect of brood age on the percent time Pintail brood hens spent surface and subsurface feeding.

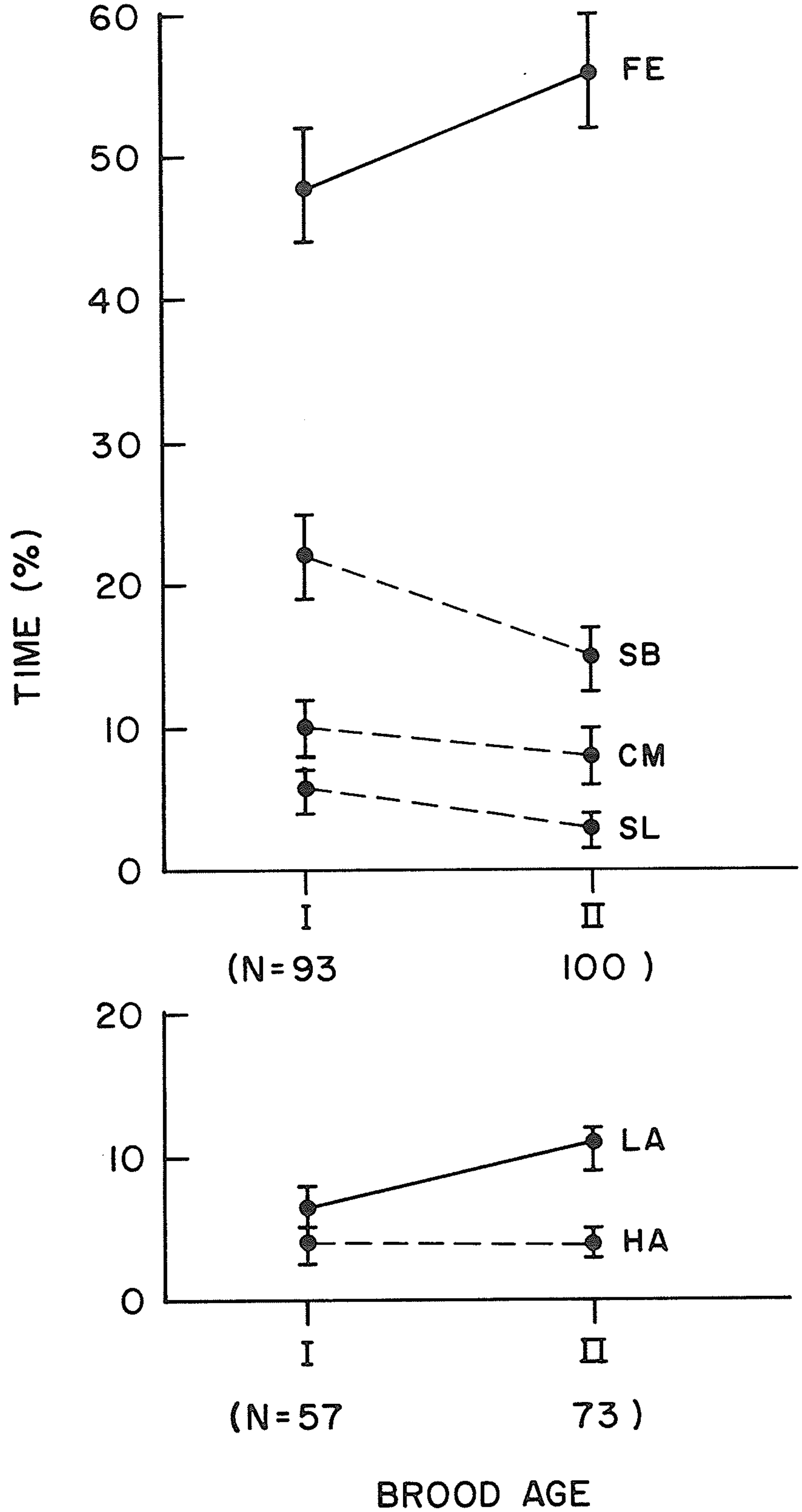

60
50
40
30
20
10
0
TIME (%)
SUB
SUR
I
II
(N=93
100)
BROOD AGE

spent more time surface feeding with downy young than with feathered young, and more time subsurface feeding with feathered young than with downy young.

Feeding styles of ducklings change with age. Surface feeding dominates during the first five days (Sugden 1973; Krapu and Swanson 1977) and is gradually replaced by subsurface feeding as the brood gets older (Beard 1964; Sugden 1973; Krapu and Swanson 1977). The diet of brood hens has been reported to be similar to that of ducklings feeding in the same habitat (Krapu 1974). If similar feeding methods are used to obtain similar foods, the shift in surface to subsurface feeding shown by Pintail brood hens, may reflect the shift in feeding styles used by ducklings. This suggests that hens with downy young are feeding in areas where food is available to their ducklings. However it is likely that these areas also met the energy demands of the hen. In pothole regions, Wood Duck (*Aix sponsa*) (Stewart 1974) and Wigeon (*Anas americana*) (Wishart, pers. comm.) hens have been observed to temporarily abandon their broods in order to feed in potholes nearby. This behaviour was thought to occur because potholes satisfying food requirements of the young did not satisfy those of the hen.

Swim behind ($F = 4.117$; d.f. = 1 and 188, $P < 0.05$), swim lead ($F = 3.897$; d.f. = 1 and 188; $P < 0.05$) and low alert ($F = 6.520$; d.f. = 1 and 125; $P < 0.01$) varied significantly with brood age (Fig. 7).

Figure 7. The effect of brood age on the percent time Pintail brood hens devoted to different behaviours.



60
50
40
30
20
10
0
FE
SB
CM
SL
TIME (%)
I
II
(N=93
100)
20
10
0
LA
HA
I
II
(N=57
73)
BROOD AGE

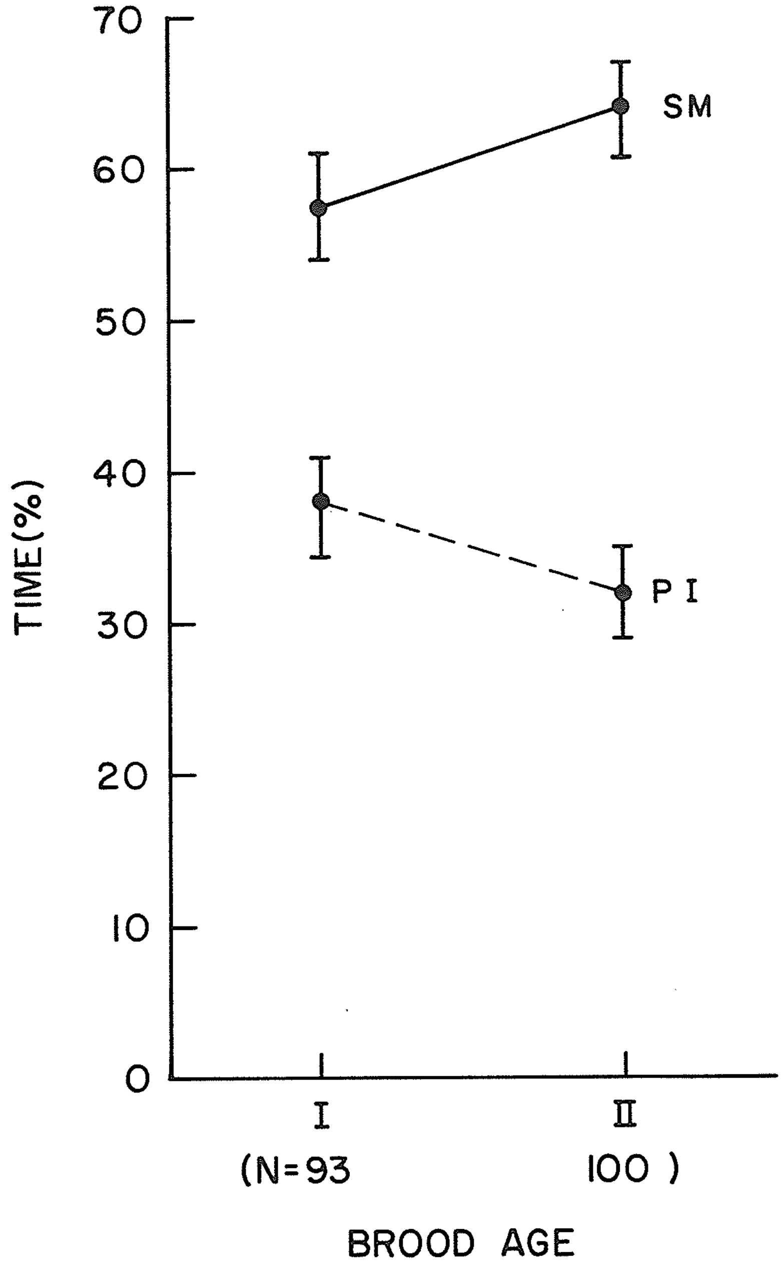
As broods got older, hens spent less time swimming behind the brood ($P < 0.005$) and more time low alert ($P < 0.01$). This shift in behaviour may have resulted from the tendency of older broods to remain in one area longer while feeding. This is possible since the entire water column plus the marsh bottom are accessible to older ducklings, while young ducklings are restricted to feeding on the surface and top portion of the water column (Sugden 1973). Hens spent more time swim leading with downy young than with feathered young ($P < 0.05$). This indicates the weakening of the hen-brood bond which is strongest in young broods (Beard 1964).

Since high alert is thought to function in watching for predators (Lazarus and Inglis 1978) one might expect that this behaviour would have decreased with brood age. Such a trend has been reported for Pink-footed Goose (Lazarus and Inglis 1978) and Ruddy Duck young (Oxyura jamaicensis) (Joyner 1977). However older goslings, being substantially larger than even adult Pintails, likely possess fewer predators than do Pintail ducklings. When on open water, diving duck young such as Ruddy Ducks, are possibly more efficient at escaping some predators than Pintail young. In response to predators, divers swim towards deep open areas (Joyner 1977), dive and emerge only their bills when they need air (pers. observation). Dive duration increases with age (Joyner 1977), making older broods less susceptible to predation. While Pintail young may also dive in response to a predator, they are not highly adapted for this behaviour. Rather than diving, Pintail young (of all ages) typically rush for cover in the nearest emergent vegetation. Consequently they are visible during escape, while divers are immediately concealed. Thus vulnerability of Pintail young to predators may remain high, despite the fact that vulnerability may decrease with brood age (Beard 1964). The areas used most commonly by Pintail hens during this study consisted of large stretches of open water with very little vegetation interspersed for cover. This feature alone may have made it necessary for hens to maintain constant vigilance. Greig-Smith (1980) postulated that predators may value larger food items more highly, and greater defence of older offspring may be necessary to prevent predation. This would be offset by the fact that older ducklings are more efficient at escaping predators than younger ducklings (Beard 1964). This hypothesis may contribute to explaining why low alert remained constant with brood age.

Barash (1975) has suggested that the amount of investment worth expending in a brood should, to some degree, be related to the amount already invested. This is particularly true later in the season when diminishing time reduces the feasibility of renesting. Thus as the brood gets older and chances of renesting decrease, protection of the brood is expected to increase to ensure reproductive success for the present season (up to a point). This trend has been described for altricial species (Barash 1975; Andersson *et al*. 1980). According to Barash (1975), although precocial young do represent a greater investment to the parent as they get older, this investment is to some extent counteracted by their increasing ability to survive without further parental investment. The fact that high alert (which is thought to function in watching for predators and hence is related to brood defence) remained relatively constant with brood age may support this theory. Stephen (1963) obtained similar results for the Mallard (*Anas platyrhynchos*). He found that the frequency of distraction displays used by females for brood defence remained approximately constant between class I and class II young.

Brood age had no significant effect on parental investment or self maintenance (Fig. 8). As the ducklings get older they become more capable of finding satisfactory feeding and loafing sites. Consequently, the benefits of swim lead would decrease (as observed) and one might expect the predicted decline in parental investment to occur. However low alert increased with brood age (if combined with high alert to form an alert category, the increase is significant at $P < 0.005$) negating the decrease observed in

Figure 8. The effect of brood age on parental investment (PI) and self maintenance (SM) by Pintail brood hens.


70
60
50
40
30
20
10
0
TIME (%)
SM
P I
I
(N=93
II
100)
BROOD AGE

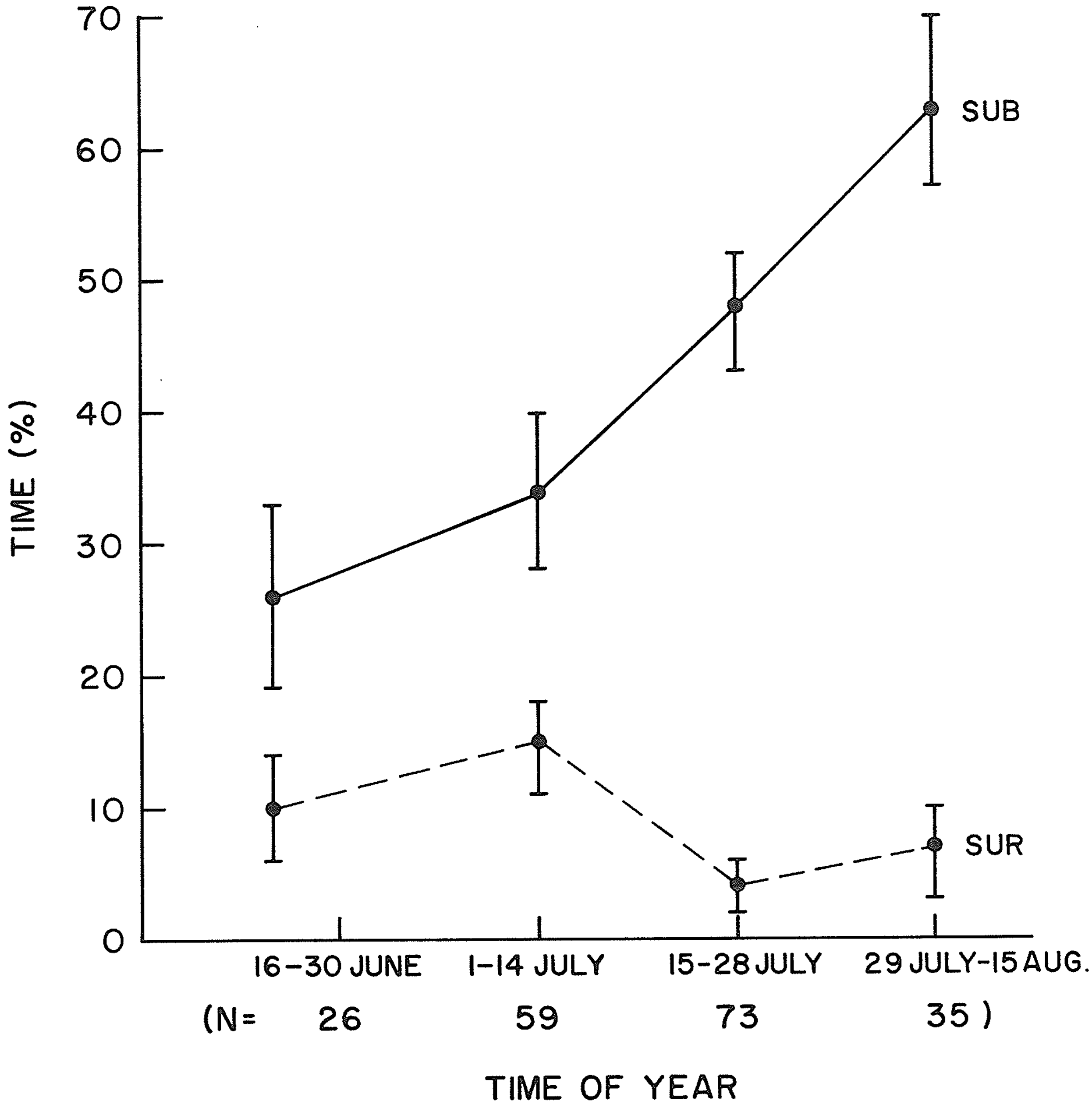
swim lead and swim behind. Thus no significant effect of brood age on parental investment was observed in Pintail brood hens.

Lazarus and Inglis (1978) observed a significant decline in extreme head up with age of Pink-footed Goose young and concluded that parental investment decreased with brood age. However it seems probable that other behaviours also contributed to parental investment. Parents were observed to run after young that had strayed and chase them back into the family. Thus monitoring the position of offspring may also be an element of parental investment in Pink-footed Geese.

Time of Year

The data were divided into four time periods approximately two weeks in length, ranging from 16 June 1979 to 15 August 1979. Time of year had a significant effect on surface ($F = 8.803$; d.f. = 3 and 186; $P < 0.001$) and subsurface feeding ($F = 11.376$; d.f. = 3 and 186; $P \leq 0.001$). Subsurface feeding increased over the season ($P < 0.001$) while surface feeding fluctuated showing a significant decrease from 1 July to 28 July ($P < 0.001$) (Fig. 9).

Figure 9. The effect of time of year on the percent time Pintail brood hens spent surface and subsurface feeding.



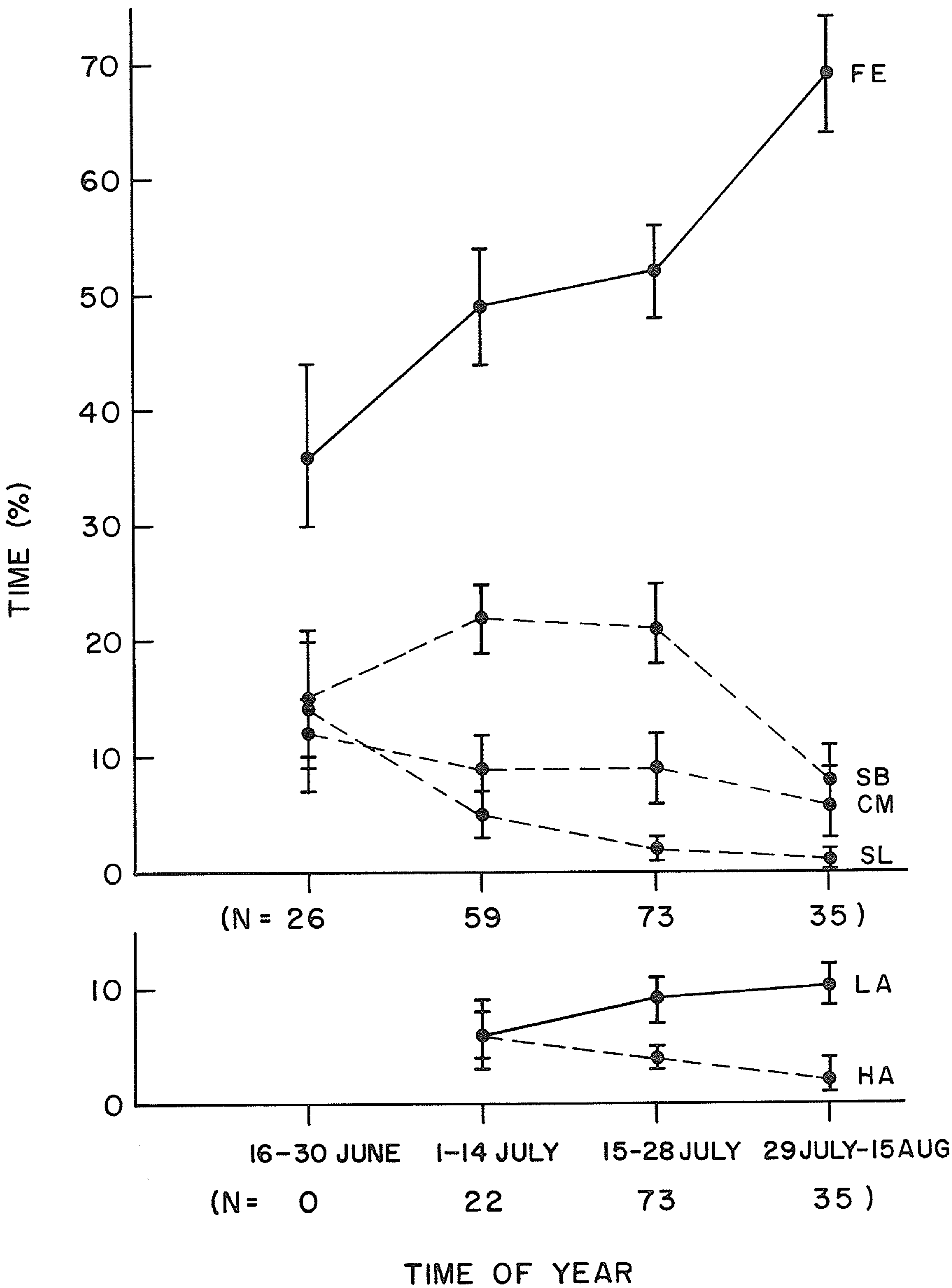
70
60
50
40
30
20
10
0
TIME (%)
SUB
SUR
16-30 JUNE
1-14 JULY
15-28 JULY
29 JULY-15 AUG.
(N= 26
59
73
35)
TIME OF YEAR

Pintail brood hens and broods spent a considerable amount of time surface feeding on algal mats that formed in the marsh, possibly straining out invertebrate material associated with the algae. These algal mats were washed ashore on 17 July due to strong winds. The presence or absence of these mats may have been responsible for the fluctuation observed in the amount of time Pintail hens spent surface feeding. Krapu (1974) reported that Pintail brood hens surface feed in late spring and summer when chironomid pupae move to the surface in large numbers. Thus hens may also have been responding to the presence of chironomid pupae.

The overall increase in subsurface feeding is a reflection of increased feeding over the season since subsurface feeding was the commonest feeding style used by Pintail brood hens (Fig. 2). Reasons for this increase will be discussed later.

Time of year had a significant effect on swimming behind ($F = 9.576$; d.f. = 3 and 186; $P < 0.001$) and swim leading ($F = 17.654$; d.f. = 3 and 186; $P < 0.001$) (Fig. 10). Swimming behind increased between 16 June and 14 July ($P < 0.05$) followed by a decrease between 15 July and 15 August ($P < 0.001$). Time spent swim leading showed an overall decrease ($P < 0.001$).

Figure 10. The effect of time of year on the percent time Pintail brood hens devoted to different behaviours.

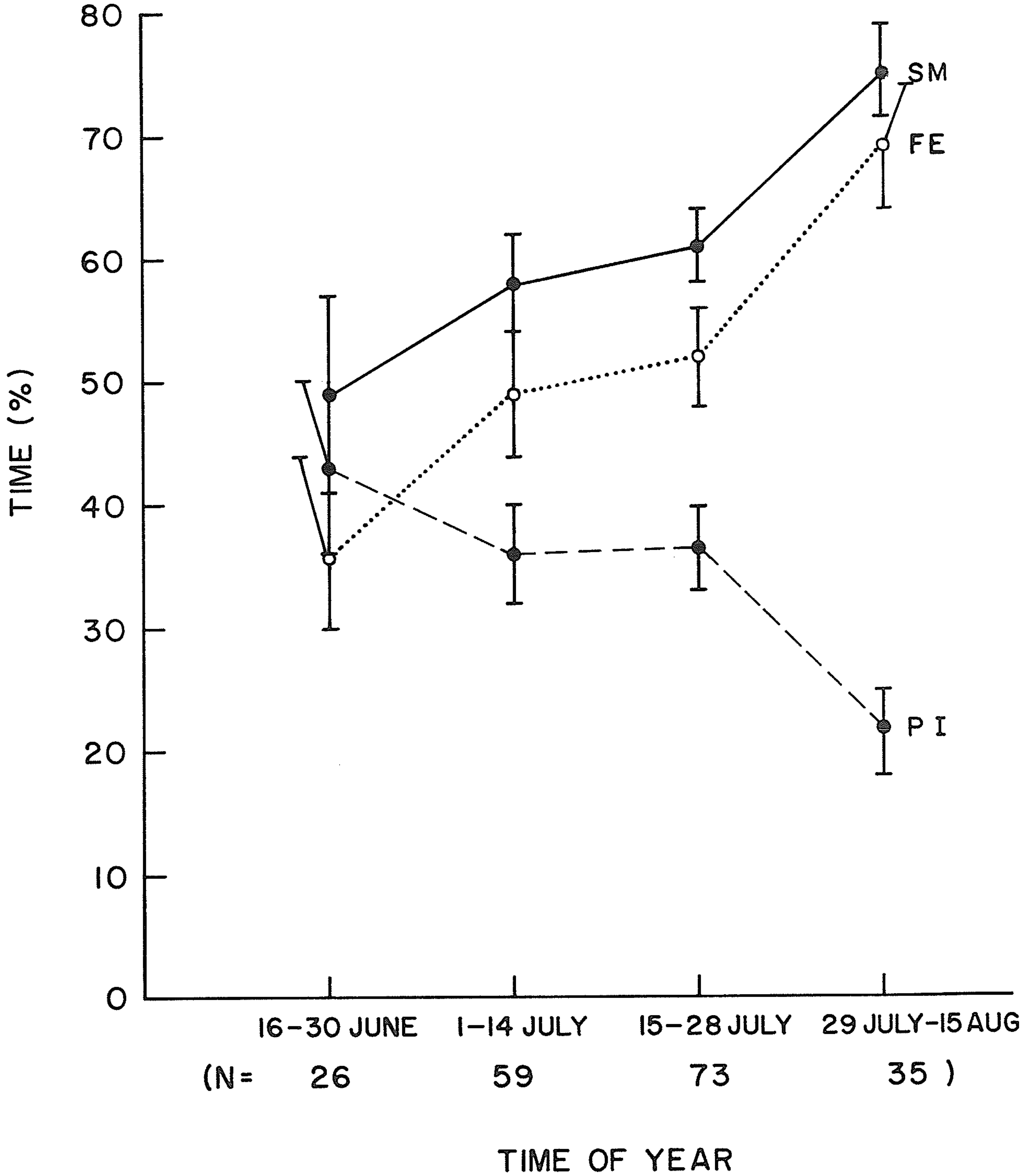

TIME (%)
70
60
50
40
30
20
10
0
FE
SB
CM
SL
(N = 26
59
73
35)
10
0
LA
HA
16-30 JUNE
1-14 JULY
15-28 JULY
29 JULY-15 AUG
(N = 0
22
73
35)
TIME OF YEAR

As the year progressed, hens spent less time leading the young to safety, to feeding sites and to loafing sites. Time spent monitoring the position of the brood was high in early July and decreased in mid-August. Thus broods reared in late July and early August received less parental investment than those reared earlier in the season.

Parental investment ($F = 9.956$; d.f. = 3 and 186; $P < 0.001$) and self maintenance ($F = 10.567$; d.f. = 3 and 186; $P < 0.001$) varied significantly with time of year (Fig. 11). Parental investment decreased between 15 July and 15 August ($P < 0.001$), while self maintenance increased between 16 June and 14 July ($P < 0.05$) and again between 15 July and 15 August ($P < 0.001$). Parental investment decreased as a result of a significant increase in feeding ($F = 12.199$; d.f. = 3 and 186; $P < 0.001$) (Figs. 10 and 11). Changes in feeding parallel those observed in self maintenance. Feeding increased between 16 June to 14 July ($P < 0.001$) and again between 15 July to 15 August ($P < 0.001$). During early to mid-July brood hens spent approximately 50% of their time feeding. By mid-August time spent feeding increased to 69%.

Pintail brood hens undergo several energetically expensive processes throughout the brood rearing and post-breeding season that may increase energy requirements. These include the prebasic molt and premigratory fat deposition.

Figure 11. The effect of time of year on parental investment (PI) and self maintenance (SM) by Pintail brood hens. The relationship between time spent feeding (FE) and time spent at parental investment and self maintenance is illustrated.



80
70
60
50
40
30
20
10
0
TIME (%)
SM
FE
PI
16-30 JUNE
1-14 JULY
15-28 JULY
29 JULY-15 AUG
(N= 26
59
73
35)
TIME OF YEAR

Both increased body temperature and metabolic rates of molting birds indicate that the molt involves increased energy demands (Payne 1972). Ankney (1979) has suggested that a bird can meet these demands by increasing daily nutrient intake, making compensatory reductions in other nutrient demanding functions or catabolizing energy. Energy consumption by Japanese Quail (Coturnix coturnix) was shown to increase significantly during the molt (Thompson and Boag 1976), and the protein requirements for molt in Lesser Snow Geese (Chen caerulescens caerulescens) are thought to be obtained through increased food intake (Ankney 1979). Since Pintail hens begin molting by late July (Bellrose 1976), increased feeding during early August may have occurred in response to energy demands of the molt. Fuller (1953) has shown that the molt in Pintail hens can overlap the end of the brood rearing period and Krapu and Swanson (1977) found that all Pintail hens collected during the brood season were in heavy body molt.

It is well established that migratory birds of many species develop large fat reserves prior to spring and fall migration (King and Farner 1959; King 1961; Williams 1965; Morton 1967; McNeil and de Itriago 1968; Owen 1970). These reserves result from a large increase in gross energy intake (King 1961; King and Farner 1959; Morton 1967; Owen 1970). Owen and Ogilvie (1979) reported that weight gains related to premigratory fat deposition in Barnacle Geese (Branta bucopsis) took from six to eight weeks. Assuming that ducks require a similar amount of time to prepare for migration, increased feeding by Pintail brood hens may reflect the deposition of premigratory fat.

Energy metabolism is known to vary with ambient temperature (Kendeigh 1969). Pintail hens may have increased feeding in response to colder nights in August. Mean minimum temperatures ranged from 16.5°C in early July to 9.4°C in mid-August (Weather data was obtained from the monthly meteorological summary produced by Environment Canada for Winnipeg, Manitoba). Gross energy intake of Canada Geese (Branta canadensis interior) has been shown to increase with decreasing ambient temperature (Williams 1965). Blue-winged Teal (Anas discors) responded to a sudden drop in temperature by decreasing or maintaining previous levels of food intake and relying on fat reserves. Feeding rates did not increase in response to low temperatures unless these temperatures prevailed longer than two days (Owen 1970).

Freshwater invertebrates, which are important sources of protein for brood hens (Krapu and Swanson 1977), show seasonal fluctuations in abundance (Anderson and Hooper 1956; Loadman 1980) and in calorific content (Wissing and Hassler 1971). Thus the amount of time Pintail brood hens spent foraging may have also been affected by the abundance, availability and calorific content of food.

Pintail brood hens responded to increased energy demands and/or to decreased prey abundance and quality by increasing feeding at the expense of parental investment. A continuation of previous rates of investment may have resulted in a deterioration of the hen's condition, reducing the probability of her surviving until the next breeding season. In theoretical terms, the cost to the parent (in terms of producing future offspring) was presumably greater than the benefit to the young.

Implications of a Late Spring

The spring of 1979 was characterized by cold weather and snow until late May, followed by sudden melting and extensive flooding. The Pintail brood rearing season ranged from early June to mid-August. According to Hochbaum (1944), the Pintail brood rearing period normally ranges from mid-May to late July, with most young being capable of flight by mid-July. Therefore during the summer of 1979, the period of parental investment is more likely to have overlapped with molt, premigratory fat deposition and reduced food abundance and quality found later in the season, than during "normal" years. Thus a significant decrease in parental investment over the year may be apparent only in years with late springs, or in normal years, may only occur in late nesting or renesting birds.

Parental Investment During Loafing Periods

Attempts to watch broods as long as possible (N = 12) lasted for an average of 3 hours with the exception of one session where I was able to observe a hen for 9 hours. Hens spent approximately 5% of their time sleeping during these observation sessions. Beard (1964) observed that sleeping accounted for 25% of the total time that broods were under observation. During loafing periods, hens usually preened followed by resting and sleeping, interspersed with periods of alert. Observations made during these periods indicated that most hens spent more time resting, sleeping and preening than guarding the brood. On one occasion a hen with 6 downy young led them into the grass along the dyke edge, presumably to sleep. Shortly after I lost sight of this group, the brood reappeared, swam for a period, and then loafed unprotected on the mudbar. The brood again entered the water and proceeded to feed approximately 10 minutes before being joined by the hen. Hens were never observed to brood their young during these periods.

Therefore, although data collected during this study involved parental investment during activities that generally took place on the open water, it does not appear to under estimate time spent investing in young. If investment had been quantified during loafing periods, self maintenance would be greater and parental investment lower than observed, with the possible exception of changes in parental investment with brood age due to brooding of young.

Absence of Brood Hens From Young

The presence of the hen with the brood, regardless of whether she may have been feeding or in some other way investing in herself, is also a form of parental investment. Constant presence with the brood ensures that the hen will be available to defend her young if necessary. Pintail hens were only observed to leave their broods 6 times during 214 observation sessions. One hen disappeared into dense dyke vegetation while her brood slept on the open mudbar (as described in the previous section). In three cases, the hen made 2 to 3 short "exercise" flights a few meters away from the brood, remaining away for only a few seconds at a time. The remaining two cases involved a hen with 5 downy young and a hen with 5 feathered young. The downy brood was joined by a male Pintail who swam behind the brood for a short period without enciting a hostile reaction from the brood hen. The male then flew away followed by the brood hen. The hen returned to the young (which continued to feed in her absence) after approximately one minute. The hen of the feathered young left her brood feeding on the open marsh and disappeared from view on an island approximately 300 meters away. Ten minutes later a lone female was observed doing comfort movements in the area where the brood hen had disappeared from view. This female left the island, joined the 5 feathered young and proceeded to swim and feed with them until the entire group reached the island mudbar and began to preen. These last two observations involve 2 different hens as substantiated by date of observation and brood age.

Inter- and Intraspecific Brood Defence

The inter- and intraspecific interactions that I observed ended in one of three ways. The attacker won when the victim retreated, a stalemate occurred when the victim fought back resulting in a retreat by both victim and attacker, or the attacker was ignored by the potential victim. "Ignore" was a true response since it was always possible to determine which bird the attacker was directing its aggression towards. The "ignore" response resulted in termination of the interaction by the attacker.

Victory and "ignore" occurred for all three intensities of interaction, however the latter usually occurred in response to a threat. An American Coot (*Fulica americana*) ignored a "peck" attack and a Mallard female with 2 downy young ignored a pursuit. Marsh Hawks (*Circus cyaneus*), Eared Grebes (*Podiceps nigricollis californicus*), American Coots and Franklin's Gulls (*Larus pipixcan*) ignored aggression more often than did ducks. Stalemate occurred in response to attack or pursuit, the victim in all cases being of equal status or size (usually other Pintails and Mallards).

The intensity of interaction most frequently employed by Pintail brood hens was pursuit (Table 1). Attacking was the second most frequently used intensity of interaction while threats were the least frequently used. In other species, attacks were the most frequent form of interaction with pursuit and threat occurring second and third respectively. The intensity of interaction used is likely the cheapest (in terms of energy) that will most effectively deter the victim.

Of 180 inter- and intraspecific interactions observed, 93.9% were initiated by Pintail brood hens, 6.1% by other species and 0.6% by Pintail ducklings.

Pintail brood hens initiated the greatest number of interactions with other Pintails (Table 2). Approximately one half of these involved young (escorted by a brood hen) that approached the attacker's brood too closely. The second highest number of interactions initiated by Pintail brood hens involved American Coots and the third highest involved Mallards. As with Pintails, Mallard young escorted by females were interacted with more frequently than Mallards of any other status. Other species with which the brood hen interacted less than 10% of the time included Blue-winged Teal, American Green-winged Teal (*Anas crecca carolinensis*), Gadwall (*Anas strepera*), Wigeon, Northern Shoveler (*Anas clypeata*), Redhead (*Aythya americana*), Lesser Scaup

Table 1. The percent occurrence of three intensities of interaction used by Pintail brood hens and other species.

	% Interactions		
Attacker	Threat	Pursuit	Attack
Pintail	25.4	43.8	30.8
brood hen	N = 43	N = 74	N = 52
Other species	20.0	30.0	50.0
	N = 2	N = 3	N = 5

Table 2. Total and percent interactions initiated by Pintail brood hens (N = 169) for the different status of each victim species.

Species	Female With Brood	Lone Female	Female Unknown Status	Lone Male	Young	Unidentified Adult	Percent
American Green-winged Teal			1	10			6.5
Blue-winged Teal			4	4			4.7
Mallard	4	2	3	2	10		12.4
Pintail	4	12	8	1	22	1	28.4
Gadwall				4		5	5.3
Wigeon				6			3.6
Northern Shoveler	1	5				1	3.6
Redhead							0.6
Lesser Scaup	1			1			1.2
Ruddy Duck				1			0.6
Unidentified duck					3	4	4.1
American Coot					2	34	21.3
Eared Grebe					3	2	3.0
Franklin's Gull					1	5	3.6
Marsh Hawk						2	1.2

(*Aythya affinis*), Ruddy Ducks, Eared Grebe adult and young, Franklin's Gull adult and young, and Marsh Hawks. Canvasbacks (*Aythya valisineria*) were the only anatid species using the study area which I did not observe Pintail brood hens interacting with.

The highest number of interactions in which Pintail brood hens were the victim, were initiated by Mallards and the second highest were initiated by American Coots. Mallards initiated interactions with ducklings more often than with brood hens (Table 3).

Inter- and intraspecific brood defence are important forms of parental investment. Lazarus and Inglis (1978) concluded that such defence reduced direct competition for food and interference during feeding, thus allowing high feeding efficiency of the brood. The majority of interactions involving Pintail brood hens also involved other Pintails or Mallards, particularly young of these species. The brood rearing periods of Pintails corresponds in time to that of Mallards (Hochbaum 1944) and duckling foods of the two species overlap considerably (Sugden 1973; Lees and Street 1974; Street 1977; Krapu and Swanson 1977). Thus Pintail brood hen-Pintail duckling and Pintail brood hen-Mallard duckling interactions may have reduced competition for food. Such competition may occur commonly with Pintail broods since some of their major foods are reported to be aggregated in clumps (Paterson and Fernando 1971). Hostility towards

Table 3. Number of interactions initiated by other species with Pintail brood hens and ducklings as victims. (N = 11).

Species	Pintail Female	Pintail Duckling
Gadwall female	1	1
Mallard female	1	3
Northern Shoveler female	1	1
American Coot	2	1

young from other broods may also function to maintain brood integrity (Frazer and Kirkpatrick 1979; Appendix 1).

Interactions with adult ducks, adult and young Eared Grebes and American Coots, and young Franklin's Gulls may have functioned to reduce interference during feeding. American Coots, being omnivorous, may also have been potential competitors for food, or because of their aggressive nature may have threatened injury to the brood. According to Gullion (1953), all vertebrates coot-sized or smaller, become victims to vicious and relentless attack when invading coot territorial waters during the coot brood season. Joyner (1977) found that 85% of Ruddy Duck interspecific brood defence involved American Coots.

Beard (1964) observed that interspecific interactions functioned in obtaining loafing sites. Such behaviour was not observed at Oak Hammock, possibly due to the abundant loafing space on nesting islands situated throughout the marsh. However Pintail brood hens frequently pecked ducks attempting to loaf too close to their young.

Interspecific brood defense also has an anti-predator function. According to Trivers (1972), defence of the brood from predators should be considered a large investment since it is associated with a high risk of mortality or injury. No successful predation attempts were observed during the study. Marsh Hawks flying over the brood caused the young to cluster around the hen and elicited threat and pursuit responses from the brood hen. Hens also threatened or pursued Franklin's Gulls which passed over the brood. A Herring Gull (Larus argentatus), once observed in the vicinity of the brood, caused the hen and brood to crouch low in sparse grass on the marsh. Black-crowned Night Herons (Nycticorax nycticorax) and Great Blue Herons (Ardea herodias) were fairly abundant on the marsh but appeared to be no threat to broods or other waterfowl. In contrast, Joyner (1977) observed that Black-crowned Night Herons always stimulated a response from Ruddy Duck broods.

Weatherhead (1979) found that Herring Gulls elicited brood defence responses in female Northern Shovelers, while Hochbaum and Ball (1978) observed a Pintail brood hen attack and wound a Franklin's Gull. Marsh Hawks (Hecht 1951; Sowls 1955; Blohm et al. 1980) and various gull species (Anderson 1965; Lynch 1975; Joyner 1977) have been reported to prey on waterfowl young. Thus Pintail brood hens were capable of recognizing and defending their broods from potential predators. This is supported by Anderson's (1965) finding that unguarded young were often preyed upon, while gulls attempting to take ducklings accompanied by a female were unsuccessful.

Human disturbance resulted in different responses from the brood hen depending on the surrounding habitat. When in vegetation or on algal mats, the hen crouched low with the brood clustered closely around her. After 5 to 10 minutes the hen quickly led the brood away from the area of disturbance. When disturbed in open water, the hens injury-feigned (Hochbaum 1944; Mendall 1958) and quacked loudly while the young scattered to safety in dense vegetation.

Interactions were usually won by birds initiating them. Of 169 interactions initiated by the brood hen, 89.9% resulted in victory, 2.3% in stalemate and 7.8% were ignored. Pintail brood hens won all interactions with American Coots with the exception of 3 in which the coot ignored the aggression. In contrast, adult American Coots dominated Ruddy Duck-Coot encounters (Joyner 1977) and a Red-knobbed Coot (Fulica cristata) dominated a Coot-Red-billed Teal (Anas erythrorhynchus) interaction (Skead 1977). Since American Coots are extremely aggressive, hens may have risked injury to themselves when defending their brood. Thus, although American Coots are smaller bodied than Pintails, the fact that Pintail hens won duck-coot interactions indicates strong capabilities of brood defence.

Bailey and Batt (1974) found that dominance among ducks in feeding zones was dependent upon body weight of each species, with Canvasbacks and Mallards at the top of the hierarchy, Redheads second and Pintails third. Pintail brood hens won all interactions with Mallard females except one that was ignored and another that resulted in a stalemate. A Pintail brood hen also won the only interaction with a Redhead. The ability to dominate interactions with larger bodied species definitely indicates strong defence of the brood.

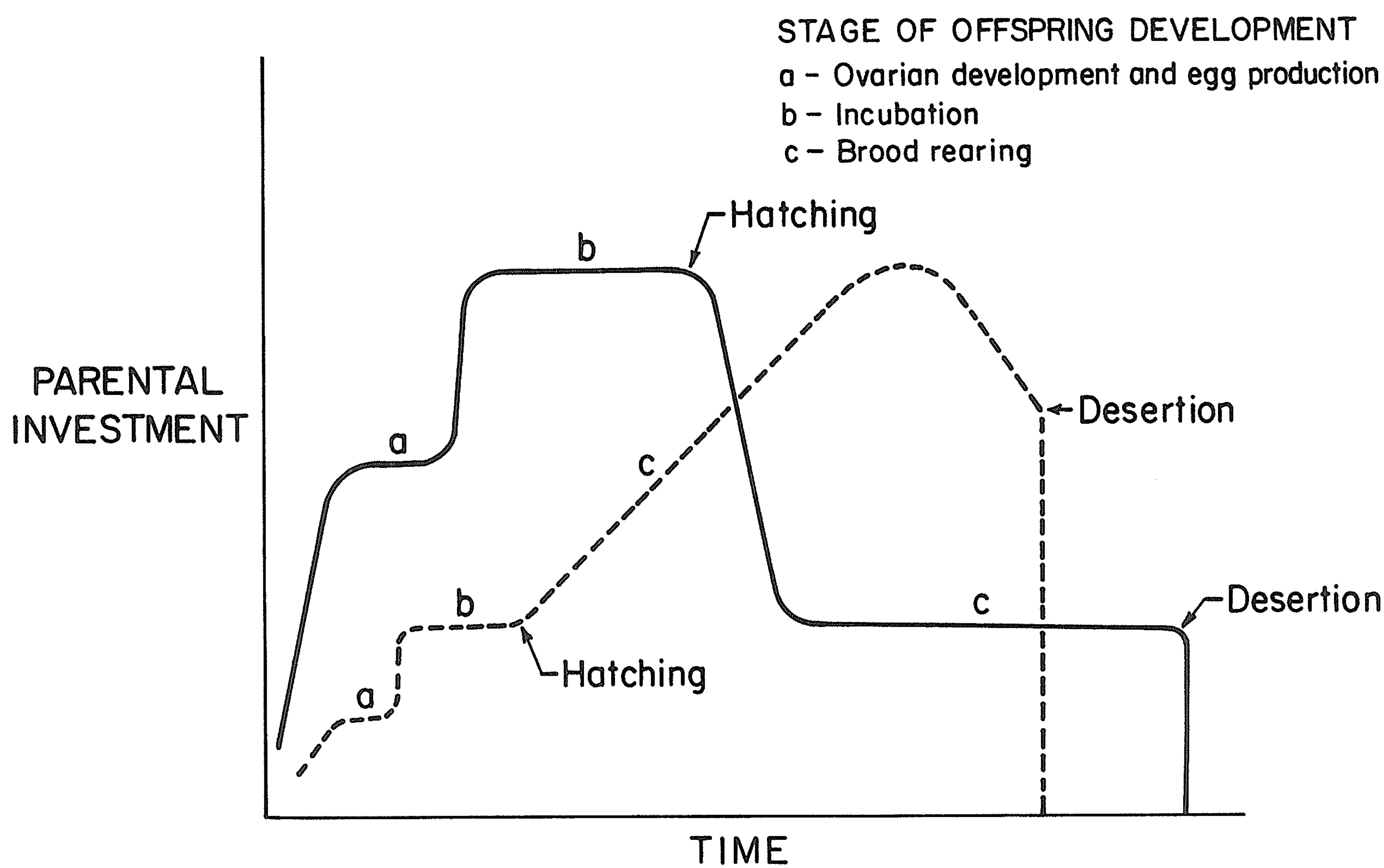
Test of Theories

Although Trivers (1972) defined parental investment as *any* investment by the parent, his predicted decline with offspring age appears to be more applicable to a species that feeds its young. The rate of parental feeding increases with brood age (Morehouse and Brewer 1968; Haftorn 1978; Smith 1978) while the young become more capable of feeding themselves. Thus the benefit of investing in the young decreases while the cost to the parent increases.

Rather than investing food energy into offspring as altricial species do, waterfowl invest large amounts of energy into eggs and the production of precocial young, many of which are already capable of acquiring their own energy. Ricklefs (1977) found that energy of a Mallard egg averaged 1.9 kcal/g while that of a Starling (*Sturnus vulgaris*) egg averaged only 1.04 kcal/g. As well as investing a large portion of reproductive energy into eggs, waterfowl also invest highly during incubation. Eggs of ducks require approximately twenty-one to twenty-six days of incubation while those of altricial young require approximately thirteen to fifteen days. Parents of altricial young expend approximately 38% of BMR (Basal metabolic rate) in energy for incubation while parents of precocial young expend approximately 153% BMR (Ricklefs 1974).

Patterns of investment over the breeding season have been illustrated for a hypothetical altricial and precocial species (Fig. 12). Altricial species do not reach maximum levels of investment until young are nearly fledged. At this point the young become capable of fending for themselves and parental investment decreases as predicted by Trivers (1974). Precocial species reach maximum levels of investment during incubation. These levels are maintained until hatching. After hatching, precocial young are capable of surviving without parental care. (However parental care greatly increases the probability of survival.) Consequently investment by the parent is decreased. This decline may correspond to that predicted by Trivers. In precocial species, parental investment is expected to decline between late incubation and brood rearing rather than during the brood rearing period as observed in altricial species. The trend for the peak energetic expense of the parent to occur after birth in altricial young and before birth in precocial young has been described by Case (1978).

Figure 12. Theoretical representation of the time and energy invested in one brood by a female of a precocial (solid line) and altricial (broken line) species during each stage of the breeding season. (Investment is not cumulative). Levels of investment are based on energy requirements calculated for different stages of the nest cycle (Ricklefs 1974) and on the amount and length of time involved in each stage (Caldwell and Cornwell 1975; Afton 1978).


STAGE OF OFFSPRING DEVELOPMENT
a – Ovarian development and egg production
b – Incubation
c – Brood rearing
PARENTAL INVESTMENT
TIME
Hatching
Hatching
Desertion
Desertion
a
b
c
a
b
c

Although parental investment was not found to increase with brood size in Pintails (this study) or in Pink-footed Geese (Lazarus and Inglis 1978) during the brood rearing season, this does not disprove the theory that larger broods require greater investment than smaller broods. The production of a large clutch requires more energy than the production of a small clutch (Ricklefs 1974). Larger clutches have been shown to take longer to incubate than smaller clutches (Cooch 1961; Hilden 1964) also indicating greater investment. Therefore larger broods will require greater parental investment than smaller broods. In precocial species this difference will occur prior to brood rearing.

Parental investment did vary with time of year as predicted, however, this pattern may occur only during years with late springs or in birds that renest.

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APPENDIX 1.

Brood Attacks by a Female Pintail

During the summer of 1979, I undertook a study of Pintail (*Anas acuta*) brood hen behaviour at Oak Hammock Marsh, Manitoba. The following interaction was recorded on 10 July between 05:30 and 07:30 hours (Central Standard Time), while I was time budgeting a Pintail hen escorting 6 downy young (brood age classification after Gollop and Marshall 1954). Shortly after beginning the time budget, I observed the hen pecking one duckling. This assault occurred three times over a three minute period. The duckling responded by diving and swimming away from the attack. After the third attack, this duckling was not observed in the vicinity of the brood in question. The hen and remaining young fed undisturbed for 10 minutes and loafed on the island mudbar for approximately one hour. At this point all the ducks loafing on the mudbar, including the hen and 5 downy ducklings, rushed to the water's edge. The hen and ducklings remained in the water and the hen was again observed pursuing a downy Pintail. This episode was repeated at approximately 10 minute intervals. In all cases the pursuit lasted from 4 to 6 seconds and the duckling fled from the pursuing hen. Following these pursuits, the unwanted duckling swam by itself for

3 minutes and then attempted to rejoin the brood. The hen pursued and attacked the duckling for approximately 10 seconds. The duckling fled, but rejoined the brood 2 minutes later. In response the hen viciously pecked the duckling, forcing it underwater twice as it struggled to resist attack. This interaction lasted approximately 8 seconds. Five young continued with the hen for the remainder of the observation period (10 minutes).

Two possible explanations may account for this behaviour: (1) the duckling was either part of the brood under observation and for some reason was unwanted by its parent, or (2) the duckling had lost its own parent and was seeking a replacement brood. Millias (1902 in Delacour 1964) reported an instance where a "tardy" duckling was pecked and killed by a female Mallard (Anas platyrhynchos), while Weidmann (1956 in Delacour 1964) stated that weak young may be killed from being pecked by the hen. The duckling in this study was not observed to be "tardy" and was obviously not weak as evidenced by its ability to survive numerous attacks. Attacks by parents on their own broods have been observed in Shelducks (Tadorna tadorna) (Hori 1964a, b). Since adult Shelducks undergo an annual molt migration, Hori (1964a) suggested that brood attacks function to break the family bond. Dabbling Duck females normally remain on the brood-rearing marsh to molt (Gilmer et al. 1977) and since only one duckling was under attack this theory does not apply.

McKinney (1967) found that penned female Northern Shovelers (*Anas clypeata*) with broods often attacked and killed ducklings from other broods. Beard (1964) observed 16 different instances of ducklings being driven away by Wigeon hens and in all but one case the unwanted ducklings were Wigeon. However if young persevered in their attempts and survived the first 3 or 4 attacks by the female, they were frequently accepted into the brood. Ring-necks (*Aythya collaris*) (Mendall 1958) and Ruddy Ducks (*Oxyura jamaicensis*) will also attack downy young attempting to join their broods (Joyner 1977).

Canvasback (*Aythya valisineria*) hens are able to distinguish their ducklings from those of other hens (Hochbaum 1944). According to Beard (1964) the hen is aware if part of her brood is missing. This suggests that she should also be aware if an extra duckling is present. Thus it appears that the sixth Pintail duckling was a stray seeking a replacement brood.

Allowing unrelated young to join the brood involves both advantages and disadvantages. If additional unrelated ducklings are mixed with the brood, the probability of the brood hen's own offspring being preyed upon would decrease. Hilden (1964) found that *Aythya* sp. hens experienced difficulty in keeping large broods intact when threatened by an enemy and when brooding in cold weather. In this case, additional unrelated young may displace the hen's own offspring during predation attempts and in competition for brooding space. Unrelated young in the brood would also compete with the hen's young for localized food resources, possibly increasing the energy and time necessary to obtain food. It is likely that the disadvantages of accepting downy young into the brood outweighed the advantages in the situation described at the beginning of this paper. However if a duckling is persistent enough, it may be more beneficial to the hen to accept it into the brood rather than waste time and energy pursuing and attacking it.

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APPENDIX 2.

The relationship between brood size and brood age for Pintail broods at Oak Hammock Marsh, Manitoba, 1979.

Brood Age	$\bar{x}$ Brood Size	N	s^2
Ia*	6.03	32	2.41
Ib	5.87	30	2.25
Ic	4.50	31	3.32
IIa	4.88	34	3.34
IIb	4.77	35	4.29
IIc	5.45	31	4.89

* Broods were aged according to Gollop and Marshall's (1954) classification system.

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