PARENTAL BEHAVIOUR AND ROLE DIFFERENTIATION IN THE BLACK OYSTERCATCHER

Haematopus bachmani

by

MARGARET ANITA PURDY
B.Sc. (Hons.) Acadia University 1976

A THESIS SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department
of
Biology

ACCEPTED
ULTY OF GRADUATE STUDIES
[redacted]
DEAN
E March 3, 86

We accept this thesis as conforming
to the required standard

[redacted]

E. H. Miller

[redacted]

P. T. Gregory

[redacted]

E. M. Hagmeier

[redacted]

M. C. Edgell

[redacted]

J. N. M. Smith

UNIVERSITY OF VICTORIA

November 1985

ABSTRACT

supervisor: Dr. Edward H. Miller

An understanding of patterns of evolution and adaptive radiation of parental behaviour within a group such as shorebirds (sandpipers, plovers and their kin) requires adequate documentation of the characteristics and existing patterns of variation in parental behaviour, both within and among species. To this end, monogamously breeding Black Oystercatchers *Haematopus bachmani* were studied on Cleland Island, British Columbia from April-September, 1982 and 1983. The emphasis of the study was a comparison of the behaviour of males and females during six stages of the breeding season. Data were collected during day-long (16-h) sampling periods on thirteen pairs, simultaneously recording the behaviour of both pair members.

Prior to egg-laying, females spent approximately 6 per cent more time foraging than did males. During this period, males were more aggressive, spending almost twice as much time in piping behaviours with conspecifics. Males were also more alert than females, as indicated by comparison of the amount of time they spent in alert standing behaviours (females 23%, males 30%), and by the shorter bouts of foraging, preening, and sitting, which were considered to be non-vigilant behaviours. Both sexes were more aggressive toward conspecifics during this period.

Males did almost all the egg-covering during egg-laying. During the first half of incubation, females incubated twice as much as males did, but the sexes shared incubation duties about equally in the latter half. There was no diel sharing of incubation between the sexes. Females incubated in longer bouts (average 58 min) than did males (39 min). During incubation, oystercatchers rarely sat when off the nest and most other behaviours showed a corresponding decrease in the percentage they comprised of the total time-budget during these stages. Males continued to respond to intruding oystercatchers even if it meant leaving the nest. This was in contrast to females, which responded to fewer of these intruders and usually did so only after their mates had responded.

Chicks were brooded almost continuously for about the first three days after hatching and intermittently until they were 15 days old. Females did almost 70 per cent of the brooding. During the brooding period, males took a dominant role in feeding and foraging for the chick, but the sexes participated equally in this after the chicks ceased to be brooded. After hatching, both sexes showed a sharp increase in interspecific aggression, particularly toward gulls. Both sexes were more alert during chick rearing stages than during previous ones, as indicated by their shorter foraging, preening and sitting bouts and the increase in the amount of time spent in alert standing behaviours. Chicks continued to be fed even after they fledged, at approximately 40 days of age.

Behind the general trends in role differentiation there was considerable inter-pair variability. This was exemplified by the arrangement of individuals in two-dimensional space by Multidimensional Scaling. These analyses showed that, prior to egg-laying and during chick-rearing stages when chicks were brooded, pair members were more similar to each other than to birds of the same sex in other pairs. In contrast, during incubation and early chick-rearing stages the sexes tended to be grouped together.

It appears that, even though males and females adopt different parental roles, parental investment is equalized between sexes over a given breeding season. When compared with other shorebirds, the pattern of the parental behaviour exhibited by oystercatchers appears to be related to their relatively large size, long-term mate fidelity, longevity, and sedentary life style.

Examiners:

[redacted]

E. H. Miller

[redacted]

P. T. Gregory

[redacted]

E. M. Hagmeier

[redacted]

M. C. Edgell

[redacted]

J. N. M. Smith

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

This study would have been more difficult to carry out if not for the contributions of many people and institutions. Foremost, I thank my supervisor, Dr. E. H. Miller. His support, selective direction and recognition of the need for my independence in this study have been respectfully appreciated. I wish to extend thanks to Dr. P. T. Gregory for acting as my "in-house supervisor" and for the advice he provided throughout this study.

Marie-Aude l'Hyver and Joan Forsberg deserve special thanks for their assistance in the field. For their assistance in the field or during other stages of this study I would like to thank Yogi Carolsfeld, Cathy Pennachetti, Rod Palm, Peggy Frank, Stephen Price, Dawn Goley and Diana Imrie. I thank Pat Konkin for his advice in relation to statistical analyses, Eugene Dean and Laura Proctor for their assistance with computer problems, and Tom Gore for his advice concerning graphs and photographs in this thesis.

I am indebted to Richard Elliot for sparking my interest in birds and for providing constructive criticism through all stages of this study.

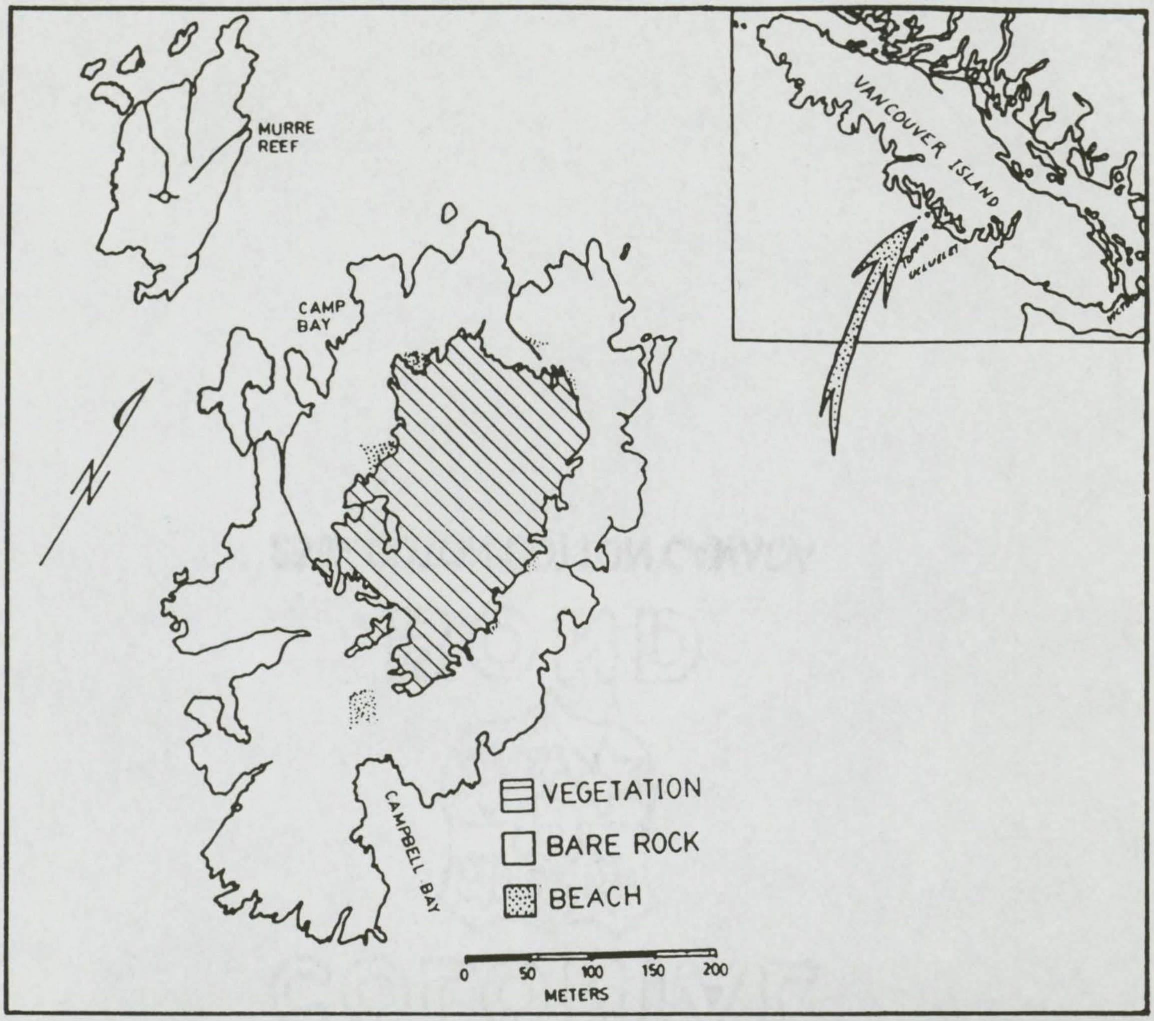
Appreciation is extended to Ecological Reserves for permitting access to Cleland Island, to Gary Kaiser of the

Canadian Wildlife Service for providing several pieces of equipment when they were needed, and to those personnel at the Tofino Lifeboat Station who maintained the regular radio schedule and kept a watchful eye on our safety in the field.

Peggy Frank did the drawings of the oystercatchers' behaviour.

This work was funded by a grant to Dr. Miller from the Natural Sciences and Engineering Research Council of Canada. Personal funding was obtained from a Graduate Research Fellowship and Scholarship from the University of Victoria. To these institutions I remain indebted.

Finally, I wish especially to thank Malcolm Macartney and Laura Taylor for providing the encouragement and advice I needed to complete this thesis.


MURRE
REEF
CAMP
BAY
CAMPBELL BAY
VANCOUVER ISLAND
UCLUELET
VEGETATION
BARE ROCK
BEACH
0
50
100
150
200
METERS

I INTRODUCTION

Parental roles vary within and across avian mating systems: male and female may share responsibilities for a single clutch; either sex may take sole responsibility or each parent may care for a single clutch. In considering aspects of the evolution of mating systems, recent authors have emphasized the importance of documenting the existing patterns of variation in parental behaviour, both within and among species (van Rhijn 1984, Walters 1984, Miller 1985).

In this respect, shorebirds (in the order Charadriiformes) provide a useful group for study. Shorebirds exhibit great diversity in parental behaviour and mating systems and, as a result, have provided significant insights into the evolution of these life-history traits (reviews by Pitelka *et al.* 1974, Lenington 1984, Oring and Lank 1984, Walters 1984). Miller's (1985) review of the characteristics of parental behaviour and role of the sexes of many breeding shorebirds suggests that these traits are conservative within this group. However, these findings are inconclusive, mainly due to the lack of detailed information on these characteristics in many species (Miller 1985). Only recently have studies of shorebirds appeared that provide the necessary quantitative information to assess adequately the variability and characteristics of their parental behaviour (Mundahl 1977, 1982, Bergstrom 1982, Erckmann 1983, Nol 1984). I have undertaken such a study on the Black Oystercatcher *Haematopus bachmani*, a monogamous shorebird in the family Haematopodidae.

Benefits and costs of parental behaviour

What options are available to parent birds to accomplish parental care, and what are the associated costs?

Prior to egg-laying, the territory and mate require protection from conspecifics. This can be achieved by active defence against conspecifics and by increased vigilance for early detection of the approach of a conspecific.

Vigilance can be defined operationally as a measure of the probability of detecting a given stimulus at a given instant in time (Dimond and Lazarus 1974), and may be considered a passive form of anti-predator behaviour (Cramp 1983). Measurement of vigilance includes several components. Birds are usually considered to be most alert when they are standing with their head and bill up, since birds in this posture can easily monitor the surrounding environment (e.g. Lazarus and Inglis 1978, Metcalfe 1984a, b). Birds are considered to be less alert when they are participating in behaviours that require attention in a specific or limited direction, such as foraging, preening, sitting, incubating, etc. Relative amounts of time and duration spent in these behaviours are taken as an indication of vigilance (Lazarus and Inglis 1978, Metcalfe 1984a, b, Metcalfe and Furness 1984, Walters 1984).

The costs to parent birds of an attack are obvious in terms of energy, but there is also the additional cost of risk of bodily injury. Costs associated with vigilance include a reduction in the amount of time devoted to the maintenance activities of preening, sleeping and foraging (e.g. Lazarus and Inglis 1978). In addition, the rapid alternation between foraging and scanning the surroundings (resulting in short foraging bouts) could result in inefficient foraging, which in turn could lead to energetic stress (Abramson 1979, Walters 1984, Metcalfe 1984 a, b; cf. Fleischer 1983).

After egg-laying, parents incubate eggs and brood chicks to protect them from adverse climatic conditions. It seems that many species do not have an added metabolic cost during incubation (review by Grant 1984). However, incubation and brooding probably limit the amount of time available for foraging (Norton 1972, Walsburg and King 1978, Maxson and Oring 1980).

Eggs and chicks also require protection from predators. This may be achieved through active defence and increased vigilance with costs similar to those outlined above for protection against conspecifics. Protection against predators may be enhanced by staying close to eggs and chicks with the associated cost of reduction in time available for foraging. Proximity to chicks may be maintained by signalling to induce following (Miller 1985) or monitoring their position and actively maintaining proximity (Walters 1982). These are essentially vigilant activities, with the associated costs.

Chicks also require food. Oystercatchers are among the few species of shorebird that feed their young. Food items are carried to young chicks at the nest and parents lead older chicks to foraging grounds where they continue to feed them. Items fed to chicks are often different from items eaten by adults (Hartwick 1973). These considerations suggest limits on adult foraging for themselves. In addition, scanning for profitable food patches or items for the young may result in inefficient foraging with the associated energetic costs.

Role differentiation

What roles do males and females take in monogamously breeding birds?

The amount of investment made by an individual is expected to be a balance between the cost associated with physiological stress and personal hazard, and the probability of reproductive success (Williams 1966). An evolutionary interpretation, based on a distribution of investment that maximizes the number of offspring produced, generates two predictions: (1) investment should increase as the egg or chick becomes older (increases in value) (Barash 1975, Curio 1975, Gottfried 1979, Andersson et al. 1980); and (2) behaviour should vary between sexes if the sexes have different options for achieving reproductive success (Trivers 1972).

Trivers' (1972) notion of "parental investment", although criticized (e.g. Dawkins and Carlisle 1976, Maynard Smith 1977, Knapton 1985), provided clarification and summary of the ideas fundamental to predicting differences in the behaviour of males and females. Parental investment is anything done for the offspring that increases the offspring's chance of survival at the cost of the parent's ability to invest in future offspring (Trivers 1972).

Differences in the behaviour of the sexes are predicted on the basis of disparity in investment, which ultimately affects the options each sex has by which to produce the maximum number of offspring in a lifetime. The parent with the greater investment per offspring will be selected to cease reproduction sooner, because the maximum number of offspring produced in a lifetime will be achieved with the production of fewer offspring. As a consequence, the sex investing less, generally the male, will adopt the strategy of seeking access to the sex investing more, generally the female. Females are usually considered to invest more per offspring than males do since they produce larger gametes and the consequences of fertilization reduces their ability to invest in future offspring to a greater extent than for males. To summarize, males have two options to maximize reproductive success: inseminate as many females as possible; and(or) provide parental care for eggs and offspring. Females can maximize reproductive success by the latter option and by obtaining the sole rights to the male's assistance. Thus, the form of investment should differ intersexually.

Parental investment theory predicts that the quantity of investment at any one time should vary according to cumulative past investment (Trivers 1972). Thus, for example, just after egg-laying, females with their greater investment (through gamete production) should theoretically be willing to invest more than their mates. This premise has been criticized on theoretical grounds. Dawkins and Carlisle (1976) proposed that further investment at any one time depends on future expectations rather than on past investment. Maynard Smith (1977) suggested that the existence of alternative options for maximizing reproductive success influences investment. These theories have been tested with differing conclusions (e.g. Weatherhead 1979, Robertson and Biermann 1979, Howe 1979).

In addition to these criticisms, there is the major practical problem of measuring investment (Pierotti 1981, Burger 1981, Mundahl 1982, Knapton 1985). Investment, which can take the forms outlined in the previous section on costs and benefits of parental behaviour, is measured currently in terms of energy investment, time investment, and(or) a risk factor (e.g. Wittenberger 1982). The problem comes in determining the relative costs of the different forms of investment. For example, which has the higher cost: the energetic and constraining influence of incubation, or the risk associated with an attack on a conspecific or potential predator, and associated cost of vigilance?

There are admittedly numerous problems with parental investment and related theories. However, I believe that they offer heuristic value in the examination of the parental behaviour of males and females. In this study I do not propose to test the predictions of parental investment and related theories, but rather use them as a guide in the study of role differentiation in breeding oystercatchers. I will compare the findings of this study with the findings of related species in an attempt to interpret the significance of the observed behaviour.

The objectives of my study are:

1) To describe and quantify the behaviour of breeding Black Oystercatchers from the prenesting stage through chick rearing, in such a way that an estimate of individual variability may be obtained.

2) To compare and contrast the behaviour of male and female Black Oystercatchers during the different stages of the breeding season.

3) To interpret the differences and changes in the behaviour in terms of factors applying to each sex and their relationship with behaviour exhibited by related species.

II METHODS

During 1982 and 1983 I studied Black Oystercatchers on Cleland Island, British Columbia (49° 10' N 126° 505'W) (Fig. 1). Data from 1982 were preliminary; those from 1983 were analyzed in detail.

Cleland Island, locally called Bare Island, is a low basalt island (average height above sea level is 10 m) about 7.7 ha in area, located 15 km off the west coast of Vancouver Island. The periphery consists of bare rock outcroppings with two small beaches composed of shell fragments. Vegetation is limited to grasses, herbs and bushes which grow on the top of the island and in rock fissures containing soil (Fig. 1). The tides are semi-diurnal and range in amplitude between extremes of 0.1 and 3.9 m. The tidal cycle advances about one hour each day.

Thirteen pairs of oystercatchers were studied in 1983. Pairs were chosen for observation if their territory could be seen from a particular vantage point. Different pairs were observed at different times in the study, because pairs that lost eggs or chicks were replaced in the sample.

Sexes were distinguished using external morphological features (Table 1) and verified by positions observed during copulation. Bands placed on some birds during previous studies, and unique body markings, served as

Figure 1: Map of Cleland Island, British Columbia.

Table 1: Criteria used to distinguish the sexes of Black Oystercatchers.

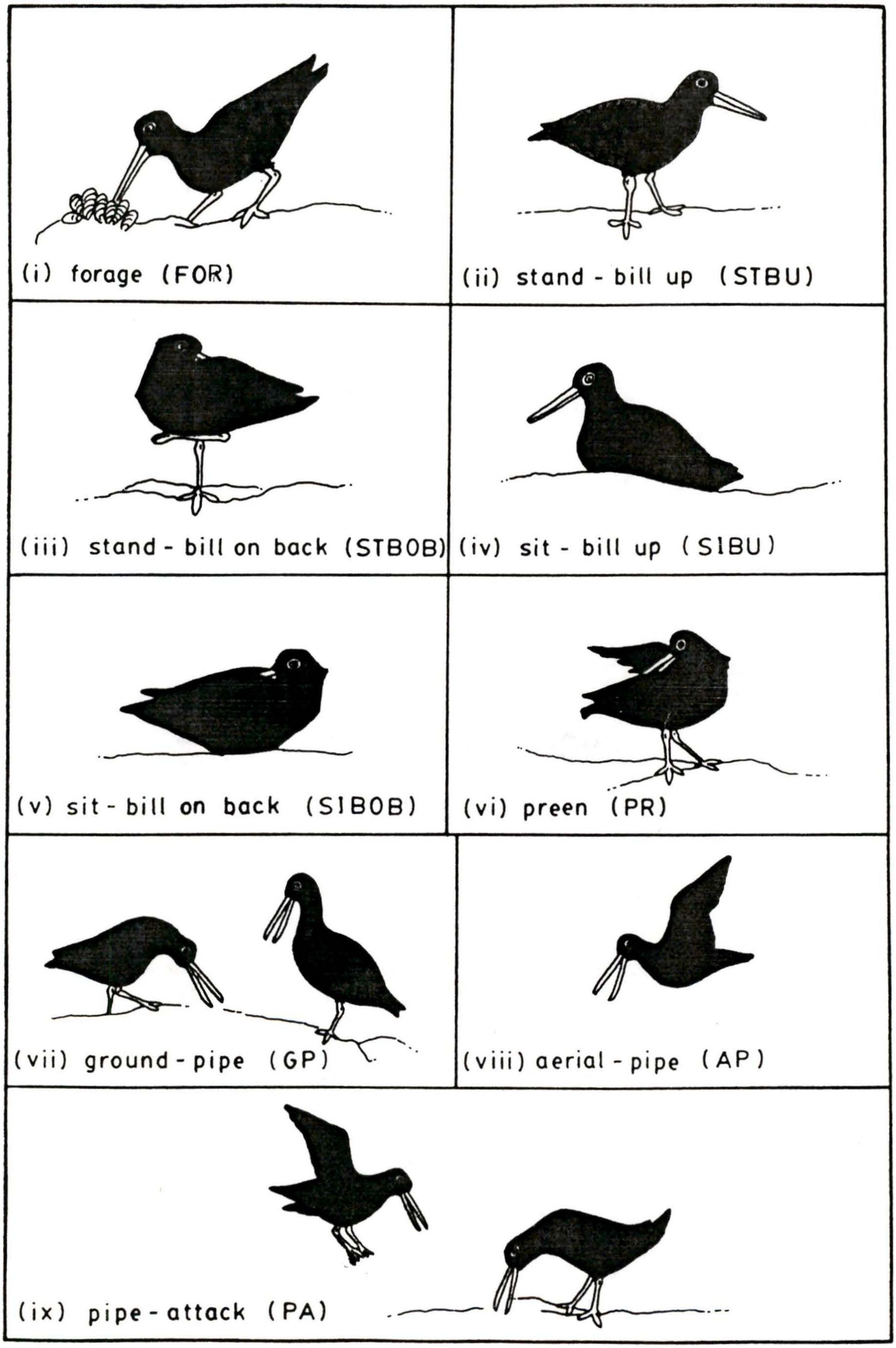
Characteristic	Species and reference
Female larger	*H. ostralegus* : Heppleston and Kerridge 1970, Hockey 1981
Female's bill longer	*H. ostralegus* : Heppleston and Kerridge 1970
	H. finschi, *H. unicolor*, *H. chathamensis* : Baker 1974
Female's bill paler orange	*H. leucopodus* : Miller and Baker 1980
Female's forehead is sloping; male's is more angular	this study
Female is browner; male is blacker	this study

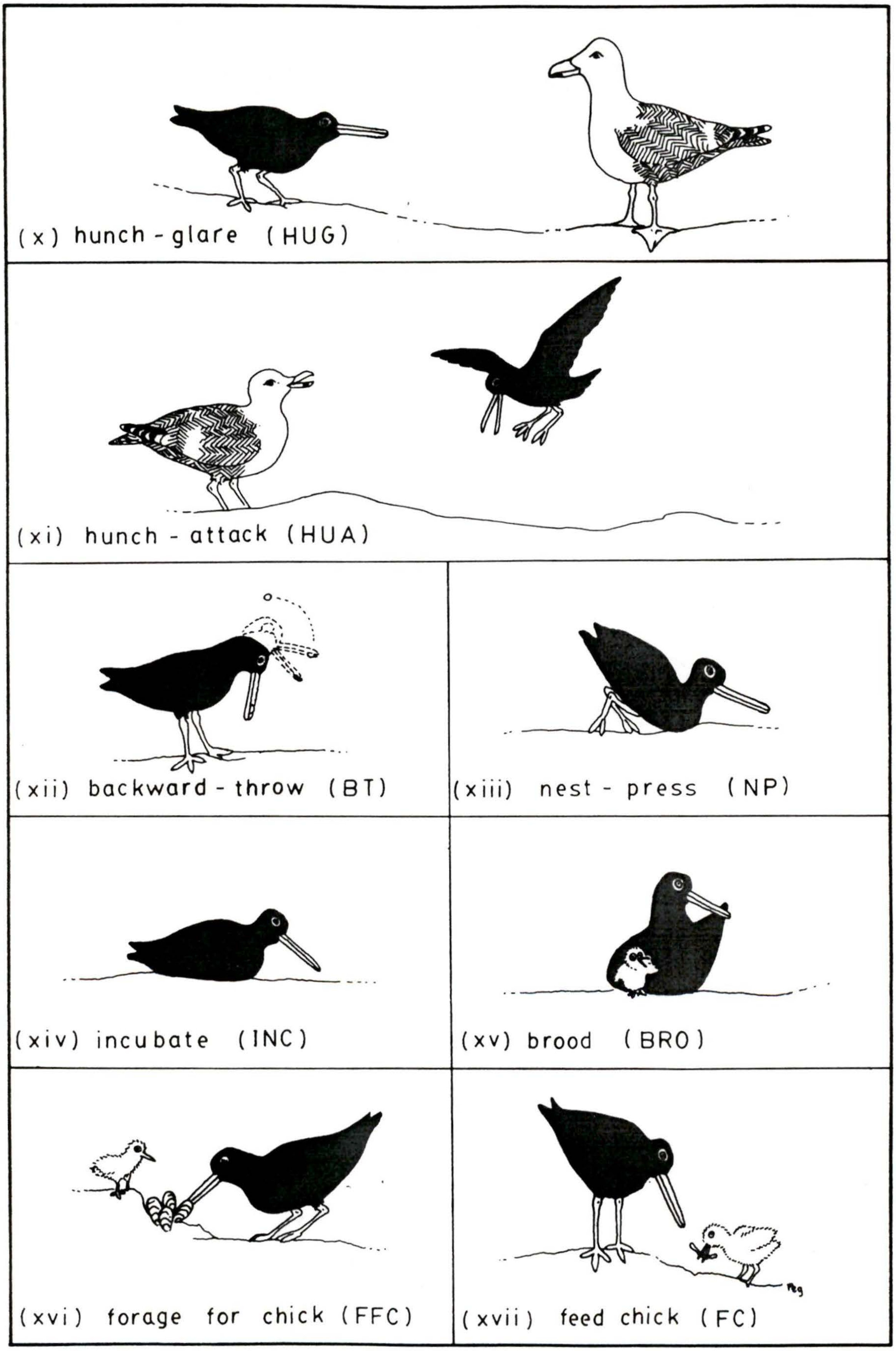
additional aids in recognizing individuals.

Observations were made from blinds using 8X40 binoculars or a 15X spotting scope. Most territories were divided into 10-m-square sequentially numbered blocks.

Data were collected for the behavioural categories illustrated in Figure 2. Observations were made during four 4-h watches per day, commencing at 0500 h. The behaviour of each pair member was recorded simultaneously during a watch. Birds were watched continuously and an entry was made each time a bird changed its behaviour or location (block); time was recorded to the nearest second. The format of data collection is shown in Appendix 1. Night observations, using a 6X image-intensifying night scope, were attempted on two occasions with limited success. These were conducted during incubation, and only the activity of the incubating oystercatcher was monitored.

Figure 2: Illustrations of behaviours.


(i) forage (FOR)
(ii) stand - bill up (STBU)
(iii) stand - bill on back (STBOB)
(iv) sit - bill up (SIBU)
(v) sit - bill on back (SIBOB)
(vi) preen (PR)
(vii) ground - pipe (GP)
(viii) aerial - pipe (AP)
(ix) pipe - attack (PA)


(x) hunch - glare (HUG)
(xi) hunch - attack (HUA)
(xii) backward - throw (BT)
(xiii) nest - press (NP)
(xiv) incubate (INC)
(xv) brood (BRO)
(xvi) forage for chick (FFC)
(xvii) feed chick (FC)

The breeding season was divided into six stages:

I (prenesting) - before egg laying began:

II (early incubation) - days 2-13 of incubation;

III (late incubation) - after 13 days of incubation;

IV (early chick-rearing) - days 1-10 post-hatching;

V (mid chick-rearing) - days 11-30 post-hatching;

VI (late chick-rearing) - after 30 days post-hatching. Data were also collected on the day eggs were laid (IIa - egg laying) and on the day chicks hatched (IVa - hatching).

To estimate how much time was required to sample behaviour adequately, the cumulative percentage of time spent in a behaviour was plotted at 1-h intervals. Figure 3 indicates that observations beyond 16 hours provided little additional information for frequently observed behaviours. For this reason, a sampling unit consisted of observations made on one pair of oystercatchers during four watches. At least one sample was obtained for each pair during a stage. If more than one sample was collected for a pair during a stage, the average of the samples was used as the estimate of the behaviour for the pair for that stage.

The four watches were usually conducted over the course of one day or on consecutive days. The day-long sampling unit was chosen because the height of the tide was expected to influence the birds' behaviour. For example, the behaviour of an oystercatcher observed at low tide would be different from the behaviour exhibited six days later conducted at the same time of day when the tide was high, simply because of the difference in the physical environments. It was hoped that this day-long sampling unit, including both high and low tides, would reduce the variability in the oystercatcher's behaviour due to tidal influence, and allow comparison of their daily activity among days with different high- and low-tide times.

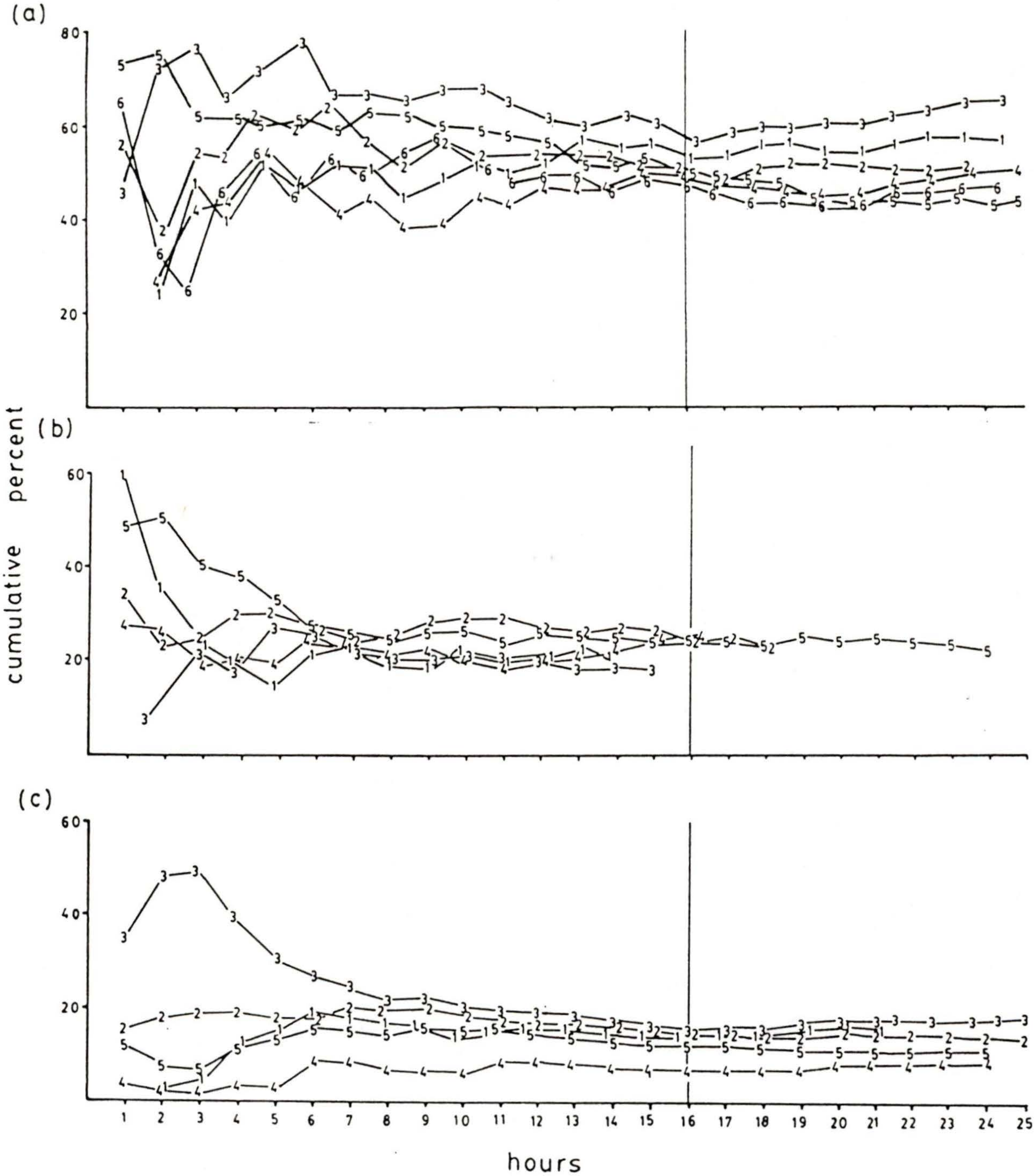
Attempts were made to watch each member of a pair for the same length of time but this was not always possible. Situations arose when birds briefly went out of sight behind rocks and obstructions while on the territory, or left the island entirely. Analyses were conducted on data recorded while the bird was in sight. Table 2 summarizes the amount of time oystercatchers were observed, and details are provided in Appendix 2.

Figure 3: Cumulative percentage of time spent in three behaviours. Numbers used as symbols indicate different individuals.

(a) Incubating by females during Stage II

(b) Foraging by males during Stage III

(c) Standing-bill up by females during Stage III


(a)
(b)
(c)
cumulative percent
hours
80
60
40
20
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

Statistical analyses

To detect differences between the sexes, I considered the number of individual oystercatchers of each sex as the sample size in most analyses. While these sample sizes are usually large enough to suggest where differences lie, they are small for statistical testing for significant differences (e.g. Sokal and Rohlf 1981). For this reason I use statistical analyses to investigate trends in the data rather than strictly testing for significance.

Behaviours were considered to be variables. For each bird, estimates were obtained for the amount of time spent in each behaviour (percentage of time), the frequency with which it was recorded and the duration of the behavioural bouts. The amount of time spent in various behaviours was expressed as a percentage of the time the bird was observed. The frequency estimates were calculated on the basis of the frequency with which a behaviour was recorded per sample. Adjustments were made to compensate for the differences in the length of time each individual was observed, by calculating the frequency of occurrence per 700 minutes. This figure was chosen because it was the mean number of minutes that individuals were in sight during each sample of four 4-h watches. Bout duration is defined as the length of time (in minutes) spent in one behavioural act. Data were manipulated to obtain each of these measures using the Statistical Analysis System (SAS) (Ray 1982).

Parametric tests were used where applicable and variances were checked for homogeneity using the F-max test (Sokal and Rohlf 1981). Data that were significantly non-homogeneous were either transformed or analyzed using comparable non-parametric tests. Differences were rejected as not differing significantly if there was greater than a 5% probability that the difference occurred by chance.

Values given in the text are expressed as the mean ± one standard error unless otherwise noted.

Members of a pair were compared using paired t-tests (Sokal and Rohlf 1981) in analyses of the differences between the sexes for each of the measures outlined above. Paired comparisons were made because the preliminary study showed that features such as territory size and quality could introduce between-pair variability that might obscure differences between the sexes.

The frequency distributions of the bout durations were also examined. Bout durations by males and females were compared within and among stages using survival analysis with the SPSSX program SURVIVAL (Hull and Nie 1979). In this analysis, bouts by each sex in a given stage were considered to be a "population". Comparisons were made

Table 2: Number of pairs of oystercatchers observed, observation period and number of hours of observation for each stage of the breeding season in 1983.

Stage		Number of pairs observed	Observation period	Total hours of observation
I	Prenest	5	April 29-May 30	182.7
IIa	Egg Laying	2	May 9-May 31	28.3
II	Incubation (day 2-13)	6	May 17-June 26	127.4
III	Incubation (>13 days)	6	June 13-July 19	162.5
IVa	Hatching	2	June 28-August 1	32.5
IV	Chick Rearing (day 2-10)	4	July 2-July 12	57.8
V	Chick Rearing (day 11-30)	7	July 9-August 16	152.8
VI	Chick Rearing (>30 days)	6	July 25-August 30	174.8

among "populations" by plotting, for each "population", the log of the remaining proportion of bouts against increasing time (Fagen and Young 1978). The resulting distributions were compared using the Lee-Desu (D) statistic which tests whether two or more sets of data have the same survivorship distribution (Hull and Nie 1979). Similar analysis has been used on behavioural data by Bergstrom (1982), Fitzpatrick (1981), and Wiley and Hartnett (1980).

To test for differences in each behaviour among the stages, the data for each sex were subjected separately to a one-way analysis of variance (ANOVA) (Sokal and Rohlf 1981). ANOVA's were conducted on each behaviour to compare percentage of time, frequency and median bout duration.

Some multivariate analysis was also used since sex-role differences are unlikely to reflect a single factor. My data failed to meet some major assumptions of most multivariate analysis, particularly because sample sizes were so low (Harris 1975). I thus performed multidimensional scaling (MDS) (Kruskal and Wish 1978). The assumptions of this test are met more easily than for many other ordination techniques, and objects are simply arranged in a multidimensional space based on their similarities or differences. The data were entered into the MDS analysis as a correlation matrix of individuals that were correlated on the basis of vectors of all behaviours. The analysis was limited to examining similarities among individuals in two dimensions, following criteria suggested by Kruskal and Wish (1978). MDS was accomplished using PROC ALSCAL in SAS (Joyner 1983).

III OYSTERCATCHER BIOLOGY

To assist in the interpretation of data presented in subsequent sections, this section provides some general information on oystercatchers based on data collected in this study.

The population of *H. bachmani* on Cleland Island overwinters in the sheltered bays and inlets within 15 km of Cleland Island (Hartwick and Blaylock 1979) and returns to the island infrequently during the winter months (pers. obs., Hartwick 1974). Cleland Island supports a breeding population of about 40 pairs of *H. bachmani* and 40-100 non-breeding individuals. Other bird species breeding on the island include Glaucous-winged and Western Gulls (*Larus glaucescens* and *L. occidentalis*), Tufted Puffins (*Lunda cirrhata*), Rhinoceros Auklets (*Cerorhinca monocerata*), Pigeon Guillemots (*Cepphus columba*), and Northwestern Crows (*Corvus caurinus*). Oystercatchers nest primarily on the exposed rocky perimeter of the island, which they share with approximately 3000 pairs of breeding gulls.

The non-breeding oystercatchers gather in a flock on the south side of Campbell Bay (Fig. 1) at night and at high tide, and were never observed to forage on the island. This flock varies in size with numbers increasing over the breeding season. Some individuals in the flock were recognizable as juveniles based on criteria described by

Baker (1974) and Harris (1967), while others were probably of reproductive age as they were banded during previous studies on the island (Hartwick 1973, Groves 1982). Some of these banded birds were present in the flock all summer, although there appeared to be turnover among the non-breeding population since certain individuals seen at the beginning of the summer were not seen again until its end. There appeared to be established pairs within this flock, because certain individuals repeatedly copulated with one another. However, copulations involving different individuals were also observed. These observations suggest that there is a surplus of adults in this population, a situation known for other species of oystercatcher (Harris 1970). I saw one copulation between a territory-holding male and a female that I was not certain was his mate; all other copulations observed were between mates.

It was possible to delineate the boundaries of most oystercatcher territories on Cleland Island. The nesting and foraging areas of most territories were contiguous, but these territories were separated by a topographical feature or another pair's territory for about five percent of the breeding population. Territories were variable in size, with six territories ranging from approximately 1200 to 6000 square meters in area, ($\bar{x}$=2867, s.d.=1700) and all pairs maintained the same territory in 1982 and 1983. Some territory holders had been banded during previous studies and had maintained the same territory for at least seven years (Groves 1982) and possibly 12 years (Hartwick 1973). Both members of pairs were on their territories upon our arrival on April 15 and the territories were maintained throughout the breeding season, even after egg or chick loss. Pairs that did not lay eggs also maintained their territories. Territory holders were not seen in the non-breeding flock until early September.

In some instances, new pairs attempted to establish and defend an area between territories of existing pairs. None was successful, although some pairs laid eggs that were either abandoned or swept away at high tide.

Most oystercatcher pairs confined their foraging activities to intertidal areas within their territory. However, some pairs flew from their territories to nearby islands, such as Blunden Island (2 km to the east of Cleland Island), during low tide, where they presumably fed.

Oystercatchers fed primarily on mussels (*Mytilus californianus*) and also took limpets (*Collisella digitalis*, *C. pelta*, *Notoacmea scutum*), chitons (*Katharina tunicata*, *Tonicella lineata*), crabs (*Oedignathus inermis*), worms (*Nereis vexillosa*) and amphipod crustaceans (*Orchestoidea californiana*, *Ligia pallasii*). Foraging usually occurred during the six-hour period around low tide.

Oystercatchers chased other shorebird species from their foraging territory. These included Wandering Tattlers (*Heteroscelus incanus*), and Black and Ruddy Turnstones (*Arenaria melanocephala* and *A. interpres*). Pigeon Guillemots and gulls were common visitors to the intertidal areas but were chased rarely by oystercatchers.

On Cleland Island, oystercatcher nests consisted of a shallow depression in the rock or shell beach lined with shell fragments or pebbles. Several nest scrapes were built on each territory and prior to egg-laying it was difficult to predict which one actually would be used. For example, during one day, one pair spent 63% of their nest-building activity at the nest scrape that was eventually used and 37% at another.

In 1982 and 1983, the average clutch size of 2.06 eggs was usually laid over a two-day period (l'Hyver pers. comm). The laying period commenced in early June and continued until mid July. Replacement clutches frequently were laid when the first was destroyed.

The incubation period averaged 28 days. Of the 201 eggs laid on Cleland in 1982 and 1983, 48% were taken by crows or gulls, and 19% were unsuccessful for other reasons, leaving 33% to hatch (l'Hyver pers. comm.).

Most oystercatchers fed mussels to their chicks, which were often brought with the shell attached; discarded mussel shells created middens around the nest. Some individuals seemed to specialize on particular food items. For example, one female fed her chicks only large worms, probably *N. vexillosa*, another brought mainly chitons (*K. tunicata*) and another brought small crabs (*O. inermis*).

Pairs that had foraging grounds adjacent to the nesting area began taking their chicks to forage when they were six to ten days old. Pairs with separated foraging and nesting areas carried food items to the nest area until the chicks could fly. Once on the foraging ground, adult and chicks formed "feeding trains" (Norton-Griffiths 1969) in which the adult fed the chicks all the food items it found. These items tended to be small, probably barnacles (*Balanus glandula*) and other small invertebrates in the mussel beds.

Seventy-one percent of the chicks (n=66) on Cleland Island in 1982 and 1983 failed to survive past ten days of age. Some of these chicks disappeared and were probably eaten by gulls, while others were found dead in the nest. The cause of death of these chicks was unknown.

None of the oystercatcher pairs on Cleland Island fledged broods of three chicks even though three eggs were often laid. Most broods consisted of a single chick although some pairs had two for a limited period. Only one pair of oystercatchers raised both chicks to fledging in the two years of this study.

Chicks fledged at about 40 days of age and continued to be fed by their parents while obtaining an ever increasing amount of food for themselves. Occasionally 60- and 78-day-old chicks were seen on their territory with their parents, which were still feeding them. Some of these chicks accompanied one or both parents on foraging trips off the island, but a 52-day-old chick was left alone on the territory for more than an hour while the adults flew to a nearby reef. By September chicks were seen in the non-breeding flock. One 70-day-old chick was seen in the non-breeding flock with the male while the female remained on the territory at the other end of the island.

The main predators of oystercatcher eggs and chicks were crows and gulls. Crows were the primary predators of eggs as indicated by the clean break in the discarded shell, often found some distance from the oystercatcher nest. Gulls were seen to take eggs but were more apt to attack oystercatcher chicks. Several chicks older than three weeks were found dead with gashes in their heads, which suggested gull predation; this was how gulls killed neighbouring gull chicks that wandered onto their territories. Oystercatchers seemed to be able to keep gulls from nesting close to their nest (distance to closest nest: gull-gull $\bar{x}$=3.3m s.d.=82 n=16, gull-oystercatcher

$\bar{x}$=4.9m s.d.=1.21 n=16; t=4.44 P<.01).

I observed attacks by adult oystercatchers on the chick of another pair on three occasions. In all cases the foreign chick was on or near the attacker's territory. The chick was viciously jabbed many times. The attacked chick called loudly, and ran away or crouched in a crevice. Attacks seemed to have little lasting effect on the chicks. During these encounters the parents called close by, and attempted to lead their chick away, but did not strike at the attacking oystercatcher.

IV RESULTS

Description of behaviours

This section includes detailed descriptions of the behaviours illustrated in Figure 2.

(i) *Forage* (FOR) - includes walking about searching for and eating food items; includes drinking; head and bill directed down.

Foraging occurred almost exclusively on the intertidal area. Oystercatchers were out of sight more often on this area than on regions of their territory above the reaches of high tide. Thus, estimates for foraging were affected most by the birds going out of sight. Since oystercatchers foraged for most of their time in the intertidal areas, I assumed that they were foraging when they were out of sight there. Those pairs that left Cleland to fly to nearby islands did so usually during periods of low tide. In addition, oystercatchers returning from such trips later in the season were carrying food for chicks. On the basis of these observations, I have considered the best estimate for the amount of time spent foraging as the combination of the time spent off the island, the time spent out of sight while in the intertidal area and the time actually recorded as foraging. Such estimates are referred to as "adjusted estimates for foraging".

Stand (ST) - standing on one or both legs; eyes open or closed.

Two distinct standing postures were recognized:

(ii) *Stand-bill up* (STBU) - standing as described above with bill held horizontal; (iii) *Stand-bill on back* (STBOB) - standing as described above with bill tucked into scapular feathers.

Sit (SI) - squatting on tarsi with body resting on the ground; eyes open or closed.

Two distinct sitting postures were recognized with head postures similar to those described above for standing: (iv) *Sit-bill up* (SIBU) and (v) *Sit-bill on back* (SIBOB).

Sitting and standing occurred on all parts of the territory but oystercatchers usually stood or sat for long periods only during high tide on favoured places within the nest area.

(vi) *Preen* (PR) - manipulation of feathers with bill; scratching and bathing.

Birds preened on all parts of the territory but long periods of preening usually occurred during high tide.

Agonistic (AG) - aggressive actions directed toward conspecifics (intraspecific aggression - *Pipe* (PIPE)) or toward other species (interspecific aggression -*Hunch* (HU))

Pipe (PIPE) - series of loud call notes, given in a typical attitude, with head and bill directed down; bill usually open; neck and shoulders hunched; bird bows repeatedly; milder forms consist of low trills without typical attitude; attack conspecific.

Three forms of piping were recognized: (vii) (*Ground-pipe* (GP) - body form as described above; exhibited on the ground; (viii) *Aerial-pipe* (AP) - body form as described above; exhibited while in flight; (ix) *Pipe-attack* (PA) - fly at conspecific and often strike it; exhibited on the ground; usually preceded by GP.

Piping was variable, appearing as a simple trill in its most mild form, and escalating to the extreme form which included parallel runs in which the performers ran side by side with short quick steps, 180° turns, head bobbing and hunched shoulders, all accompanied by loud trills. Mild piping occurred most often during meetings between members of a pair, such as when one returned to the nest site. It also took place during encounters between distant oystercatchers in response, for example, to an oystercatcher flying overhead or piping heard in the distance. Intense piping was reserved for close encounters with other oystercatchers, especially other pairs. Bouts of piping were interspersed with parallel runs and periods in which the participants stalked silently around each other. In the analysis, oystercatchers were recorded as piping only when actually vocalizing. Stalking interludes were sometimes interrupted by bouts of BT (see below and Figure 2), and I saw one individual hide its bill among its scapulars after a particularly fierce exchange (described by Makkink (1942) as "pseudo-sleep", see also Gochfeld 1984). While most encounters ended with the departure of the intruder(s), some were long and often included physical attacks (PA). The lengthy encounters usually occurred in the early part of the breeding season between neighbours near the territory boundary, and ended when both pairs eventually returned to their respective territories. Piping took place on the nest area and on the foraging area within the territory. It occurred at night, usually on the foraging grounds.

Piping seemed to be contagious. When a pair of oystercatchers heard piping in the distance, they often became alert and sometimes began to pipe. This contagiousness was particularly evident in the flock of non-breeding birds. One piping oystercatcher in this flock usually stimulated a wave of piping to spread through the group, often climaxing in part of the group taking flight, forming a "piping party" (Huxley and Montegue 1927). These piping parties were often joined by territory holders (AP) as the group flew over the island.

Hunch (HU) - head and shoulders pulled in toward body; tail lowered; body crouched; approach or attack gull or crow.

Two forms of this behaviour were recognized: (x) *Hunch-glare* (HUG) - body form as described above; bird is still or moving slowly toward predator; (xi) *Hunch-attack* (HUA) - fly at predator and often strike it; usually follows HUG.

HUG was directed most often at gulls; crows were usually attacked (HUA). A particular call ("ka-ka-que") was invariably uttered in interactions with gulls; the call was given at an increasing rate and became louder as the gull approached. Oystercatchers also "false-incubated" (squatted as if incubating) (Gochfeld 1984) during encounters with gulls, but this was rare. It usually occurred after a sudden move by the gull toward the oystercatcher. Almost all exhibitions of HUG and HUA were in the vicinity of the nest or on the intertidal area when a potential predator approached the chick.

Parental Care (PC) - actions associated with the nest, eggs and chicks.

Included in parental care: nest building, incubating, brooding, feeding and foraging for the chick.

Nest-build (NB) - actions that result in nest construction.

Two forms of nest building were recognized:

(xii) *Backward-throw* (BT) - picking up small fragments of shell or pebbles and throwing them to the side and backward. (xiii) *Nest-press* (NP) - pushing on substrate with breast and pivoting from side to side while simultaneously kicking backward with feet.

An oystercatcher usually began BT at the nest, and then continued to throw fragments while walking away. Since oystercatchers lined their nest with shells and pebbles this activity probably helped to move the fragments to the nest. BT was interspersed with bouts of NP. Both behaviours occurred at all scrapes including those eventually used as the nest. The behaviours usually appeared when both members of a pair were close to the nest. BT was most common before egg laying, but oystercatchers relieved of incubation duty often left the nest exhibiting BT. This behaviour also occurred infrequently away from the nest, during interactions with other oystercatchers.

(xiv) *Incubate* (INC) - all types of shelter- or heat-providing behaviour directed toward eggs; eyes open or closed; bill held horizontal or tucked into scapular feathers.

Incubating was often interrupted when the incubating oystercatcher stood up or moved off the nest for only a few minutes before resuming incubation. For analyses, successive periods of attendance by one pair member, without intervening attendance by its mate, were considered to be a single bout. Bouts that were ongoing at the end of a sampling period were not included unless their length exceeded any others performed by the individual in that period.

Both members of a pair incubated and several change-overs could occur in a tidal cycle. During these change-overs the relieving oystercatcher often emitted a soft purring call as it slowly walked off the nest. During hot periods of the day, oystercatchers often stood over their eggs with their mouths open. Oystercatchers frequently stood up to re-orient themselves or turn the eggs before resuming incubation.

Incubating oystercatchers piped from the nest, provoked by a piping oystercatcher passing overhead or in response to their mates. An oystercatcher that had been incubating for an extended period and whose mate was away foraging, sometimes stood beside the nest piping loudly. At other times these individuals flew over the territories piping loudly and returned within a few minutes to the nest. These bouts of piping were not accompanied by the usual body posture but simply consisted of a loud trill. This calling usually resulted in the return of the non-incubating bird and the departure of the relieved mate.

(xv) *Brood* (BRO) - all types of shelter- or heat- providing behaviour directed toward chick; eyes open or closed; bill held horizontal or tucked into scapular feathers.

Newly hatched chicks were brooded under the adult's body while older chicks were brooded under its wing. As with incubating, successive periods of brooding by one pair member, without intervening attendance by its mate, were considered to be a single bout.

(xvi) *Foraging for chick* (FFC) - any foraging behaviour that results in feeding chick.

This definition tended to be operational rather than functional, for if the adult swallowed a food item it was recorded as foraging for itself. Often adults alternated between swallowing food and feeding the chick, making it difficult to record either behaviour. Also, chicks on the foraging grounds were often fed so rapidly that it was impossible to record the intervening foraging bouts.

Consequently, not all feed chick (FC) records (see below) were preceded by FFC. For these reasons, measurements for this behaviour should be considered rough estimates only.

(xvii) *Feed chick* (FC) - holding food item in the bill which is motionless and close to the ground until the chick takes it.

Young chicks (<10 days old) were fed items brought to the nest site while older chicks were fed on the foraging ground.

Walk (WA) - walking about without pecking at food or drinking.

Fly (FL) - normal horizontal flying, no vocalization.

Walking and flying were not considered in the following analyses of behaviours. Walking and flying accounted for less then two percent of the time budget of most oystercatchers (Appendix 3). They were components of other behaviours (e.g. AP and FOR) and were not otherwise recorded routinely, thus making estimates for them highly variable.

Copulation (COP) - behaviours associated with cloacal contact.

These are summarized as follows: When advancing toward the female, the male assumed a low crouched posture with the head lowered and well drawn into the body, often emitting a soft "pic-pic-pic" call. The female adopted an attitude with the head extended and tail raised, so that the body was horizontal, exposing the cloaca, which often protruded. The male raised into an erect posture when near the female and jumped onto her back with raised wings as if for balance. Coitus lasted approximately 5 seconds after which the male jumped off to the side. No post-copulatory displays were seen. Both birds shook their tails after copulation and often preened. Copulations occurred on the foraging and nesting areas of the territory, and were observed at least two weeks prior to egg laying, two hours before laying and three days after a full clutch of three eggs was completed. Some oystercatcher pairs copulated as early as two hours after losing their clutch to predation.

Differences between sexes and among stages

In this section, I consider behavioural differences between the sexes at each stage of breeding, and changes in their behaviour over the breeding season. Comparisons were made using data summarized in Appendix 3, 4 and 5.

Forage (FOR)

The stage of the breeding cycle significantly influenced the amount of time oystercatchers foraged, and where they foraged (on their territory or off the island). Generally, oystercatchers foraged more and spent more time foraging off the island before the eggs were laid than they did during subsequent stages, and the least just after hatching (Fig. 4a, d, 5a). Males and females showed similar changes through the breeding season, but differed when they were compared within stages (Fig. 4a, 5a).

Before egg laying, females spent more time foraging than their mates did (Fig. 4a, d). This was mainly because females foraged more often than males did and their foraging bouts also tended to be longer (Figs. 4a-d, 6). The brevity of a foraging bout may reflect alertness; thus the higher percentage of short foraging bouts by males suggests that males were more alert than females at this time (Fig. 6).

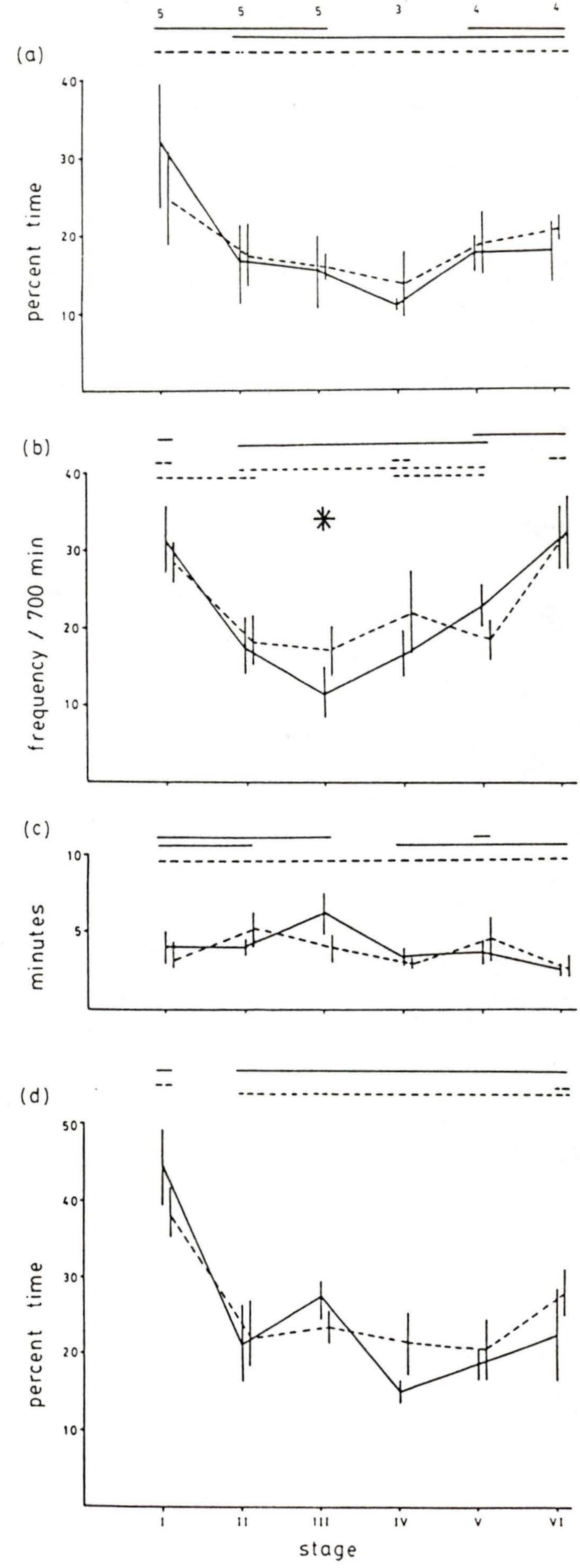
Figure 4: Comparison of the percentage of time, frequency and median bout duration of FOR by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. Significant paired t-test values are indicated (*). Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

(a) percentage of time spent FOR

(b) frequency / 700 minutes of FOR

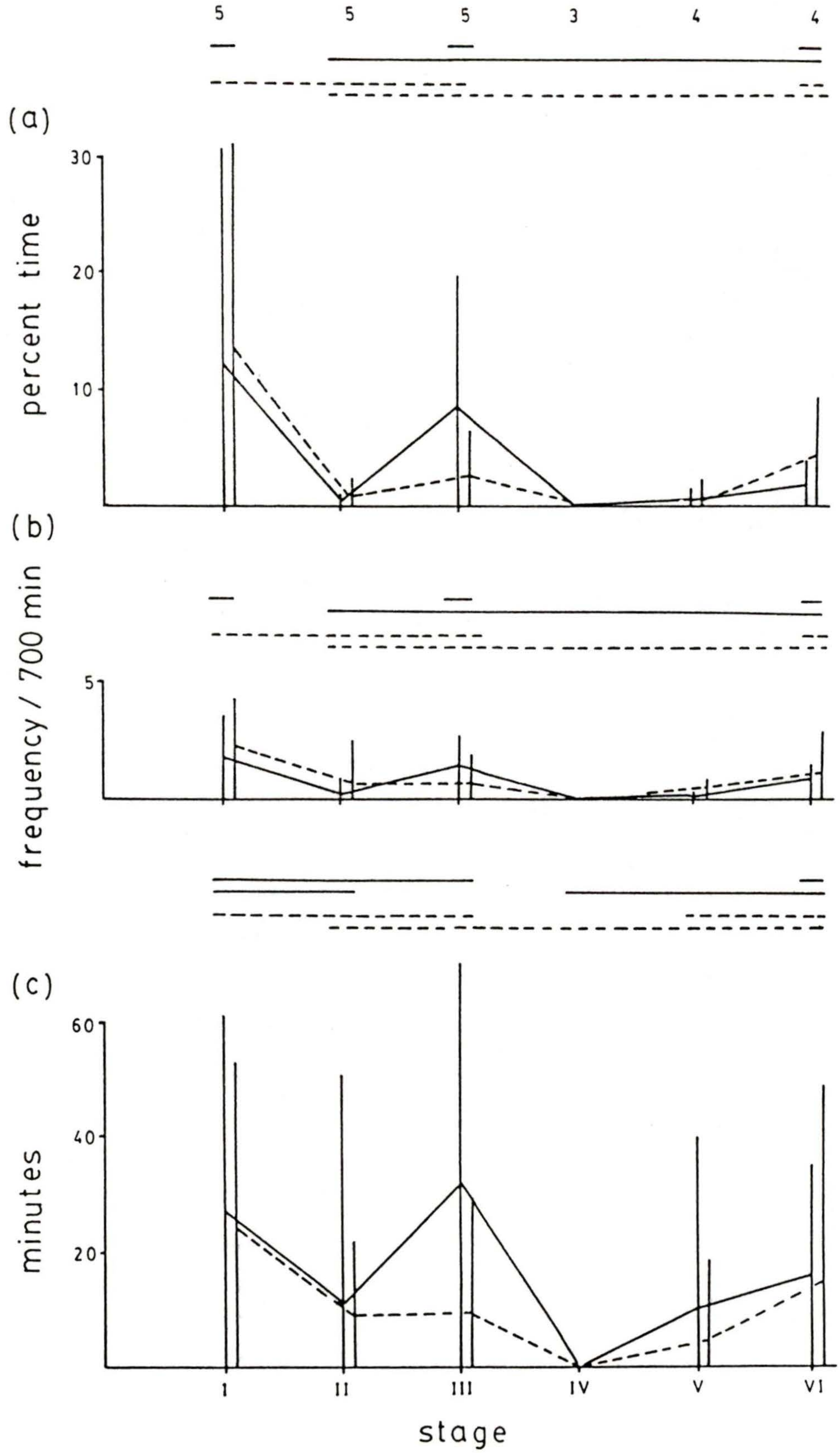
(c) median bout duration of FOR

(d) percentage of time spent adjusted FOR.



5
5
5
3
4
4
(a)
percent time
40
30
20
10
(b)
frequency / 700 min
40
30
20
10
(c)
minutes
10
5
(d)
percent time
50
40
30
20
10
I
II
III
IV
V
VI
stage

Figure 5: Comparison of the (a) percentage of time, (b) frequency and (c) median bout duration of "off territory" by male (----) and female (——) oystercatchers. Vertical bars represent ± range. None of the paired t-test values for intersexual comparisons within stages indicated significant differences. Means joined by horizontal lines on the same level are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.


5
5
5
3
4
4
(a)
30
20
10
percent time
(b)
frequency / 700 min
5
(c)
60
40
20
minutes
I
II
III
IV
V
VI
stage

During the prenesting stage 80 per cent (n=10) of the oystercatchers frequently left the island to forage. Mates usually left and returned together, so the sexes were similar in all three measures (Fig. 5a-c).

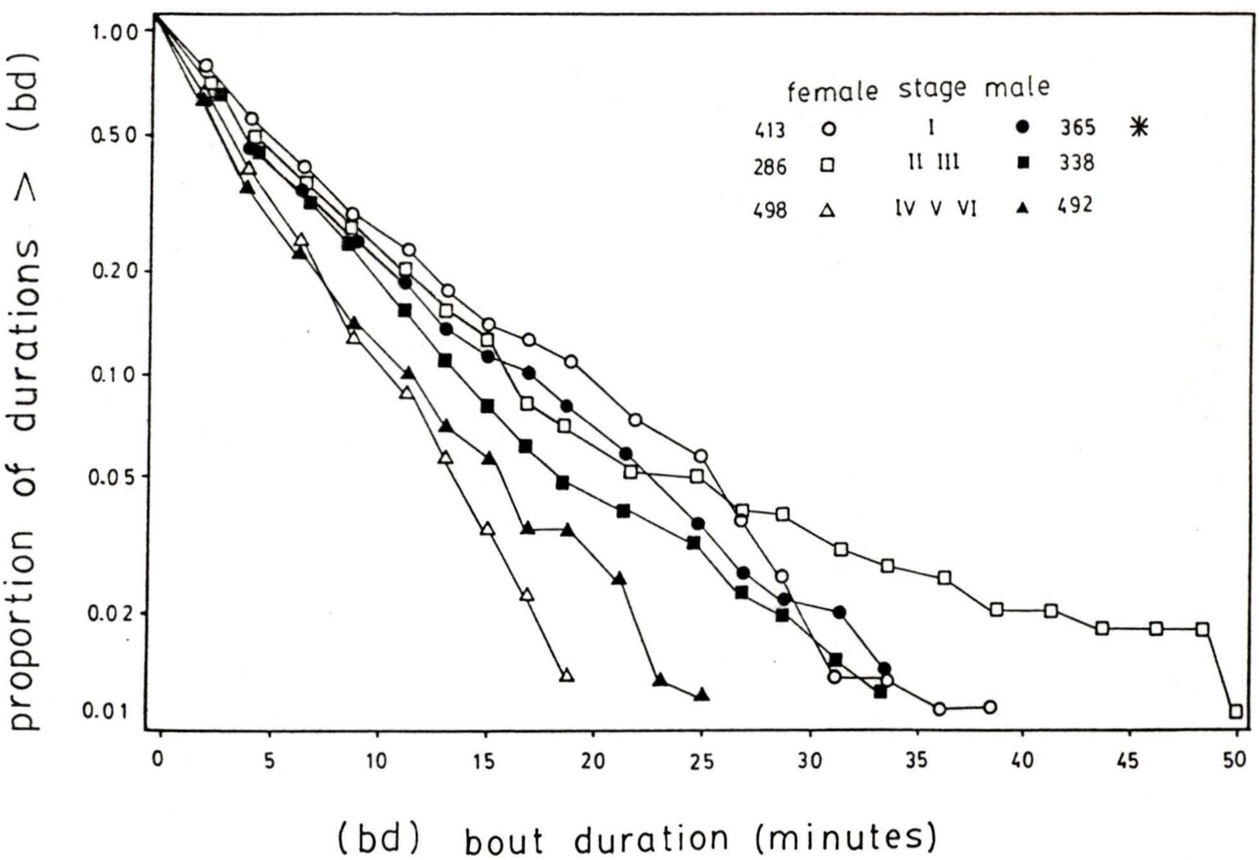
The amount of time spent foraging decreased significantly after the eggs were laid, and males and females were similar in the amount of time spent foraging throughout incubation stages (Fig. 4a, d). This decrease reflects a reduction in the number of foraging bouts, which tended to be slightly longer than during the prenesting stage (Fig. 4a-c, 6). This was particularly evident for females that exhibited a higher percentage of long foraging bouts, suggesting that in this stage too, females were not as alert as males were (Fig. 6).

During incubation stages, both members of a few pairs left the island to forage, but were never absent together. Females left more often than males did and they stayed away for longer periods (Fig. 5a-c).

The amount of time oystercatchers spent foraging continued to decrease after hatching (Fig. 4a, d). However, there was a slight increase in the frequency of foraging bouts suggesting that bouts had decreased in length as shown in Figure 4c.

None of the oystercatchers with newly hatched chicks

Figure 6: Comparison of frequency distributions of FOR bout durations of male and female oystercatchers. Significant Lee-Desu values for intersexual comparisons within stages are indicated (*). Numbers in symbol legend indicate the number of bouts included in the sample.


proportion of durations > (bd)
1.00
0.50
0.20
0.10
0.05
0.02
0.01
female stage male
413 I 365
286 II III 338
498 IV V VI 492
0 5 10 15 20 25 30 35 40 45 50
(bd) bout duration (minutes)

(Stage IV) left the island to forage (Fig. 5a-c).

Once the chicks joined the adults on the foraging ground (Stage V and VI), the adults increased the amount of time spent foraging but males tended to spend slightly more time foraging than did females (Fig. 4a, d). Generally, this increase continued gradually as the chicks grew older but the frequency with which oystercatchers engaged in foraging bouts increased sharply (Fig. 4a, b). This implication of shorter foraging bouts was verified by examining the frequency distributions of foraging bout durations, which showed that oystercatchers with chicks had shorter foraging bouts than they did in previous stages (Fig. 6). This suggests that oystercatchers with chicks tended to be more alert than they had been during incubation or before the eggs were laid. Generally, females had longer foraging bouts than males, suggesting that they were not as alert as males were (Fig. 6).

Adult oystercatchers again left the island to forage once the chicks were older than ten days (Stage V and VI). During Stage V one male and one female (from different pairs) left the island but they did not leave as often or for as long as they had during previous stages (Fig. 5a, b). Oystercatchers with fledged chicks were often joined by their chicks on these off-island foraging trips. Most of the time the chick was accompanied by both parents, although, in some cases, males accompanied the chick alone while the female remained on the territory.

Stand (ST)

Males spent more time than females in alert standing postures during most stages of the breeding cycle (Fig. 7). This trend was evident in both standing postures (Fig. 8a, d). For STBU this difference was due to the higher frequency with which males exhibited this behaviour rather than longer bout durations (Fig. 8a-c, 9). Similarly, males engaged in STBOB more often than females did, but males' STBOB bout durations tended to be longer than females' (Fig. 8d-f, 9).

Generally, males and females exhibited similar patterns through the breeding season in the amount of time they spent ST (Fig. 7). Oystercatchers with chicks spent more time ST, and were thus considered to be more alert than oystercatchers in previous stages (Fig. 7). Oystercatchers spent the least time standing during incubation, although males differed from females in maintaining levels similar to prenesting until the second half of incubation (Stage III) (Fig. 7).

Finer analysis indicated that this pattern of a decrease in the percentage of time spent standing during incubation,

Figure 7: Comparison of percentage of time spent in ST by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. Significant paired t-test values for intersexual comparisons within stages are indicated (*). Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

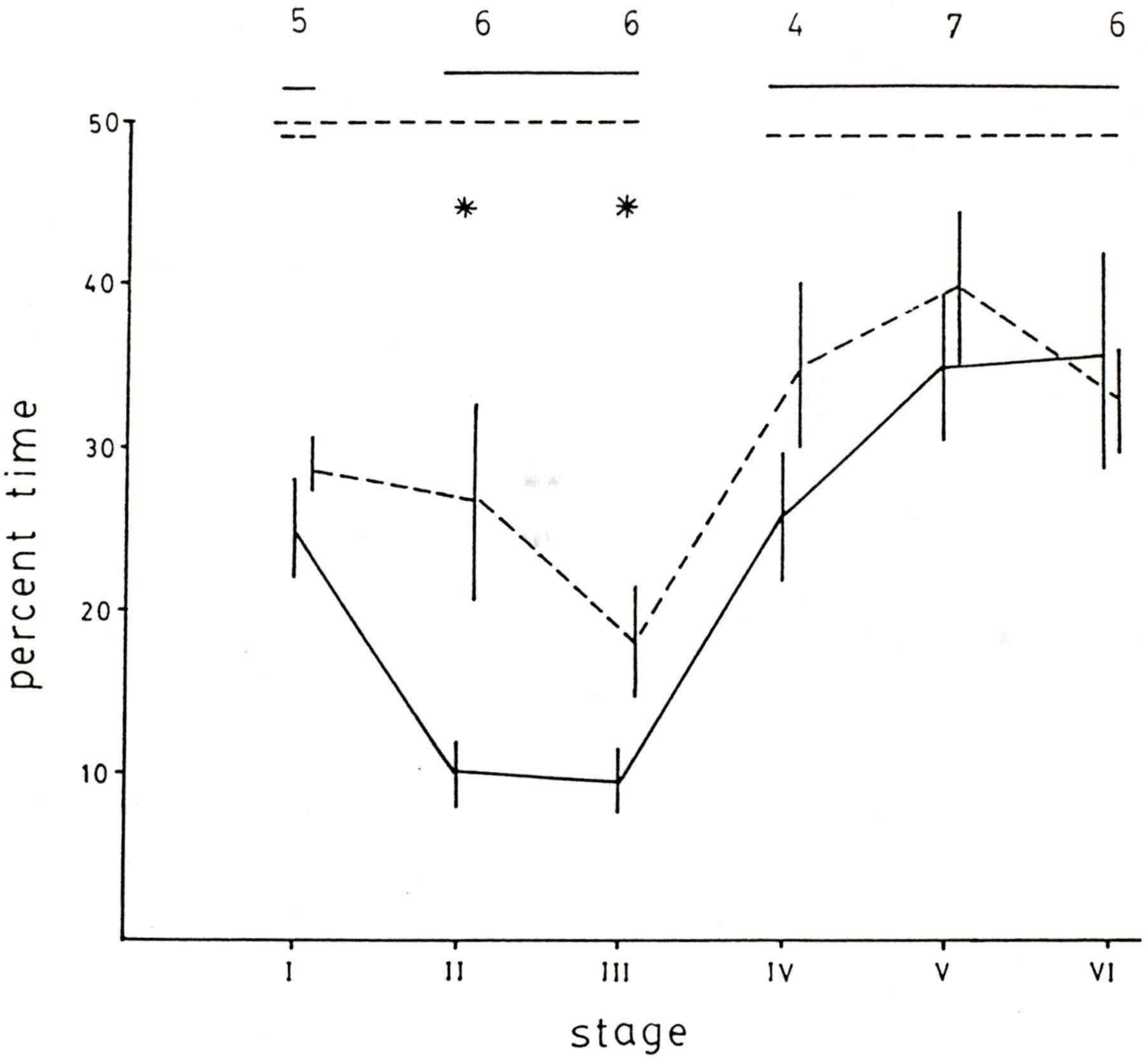

5
6
6
4
7
6
50
40
30
20
10
percent time
I
II
III
IV
V
VI
stage

Figure 8: Comparison of percentage of time, frequency and median bout duration of STBU and STBOB by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. Significant paired t-test values for intersexual comparisons within stages are indicted (*). Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

(a) percentage of time spent STBU

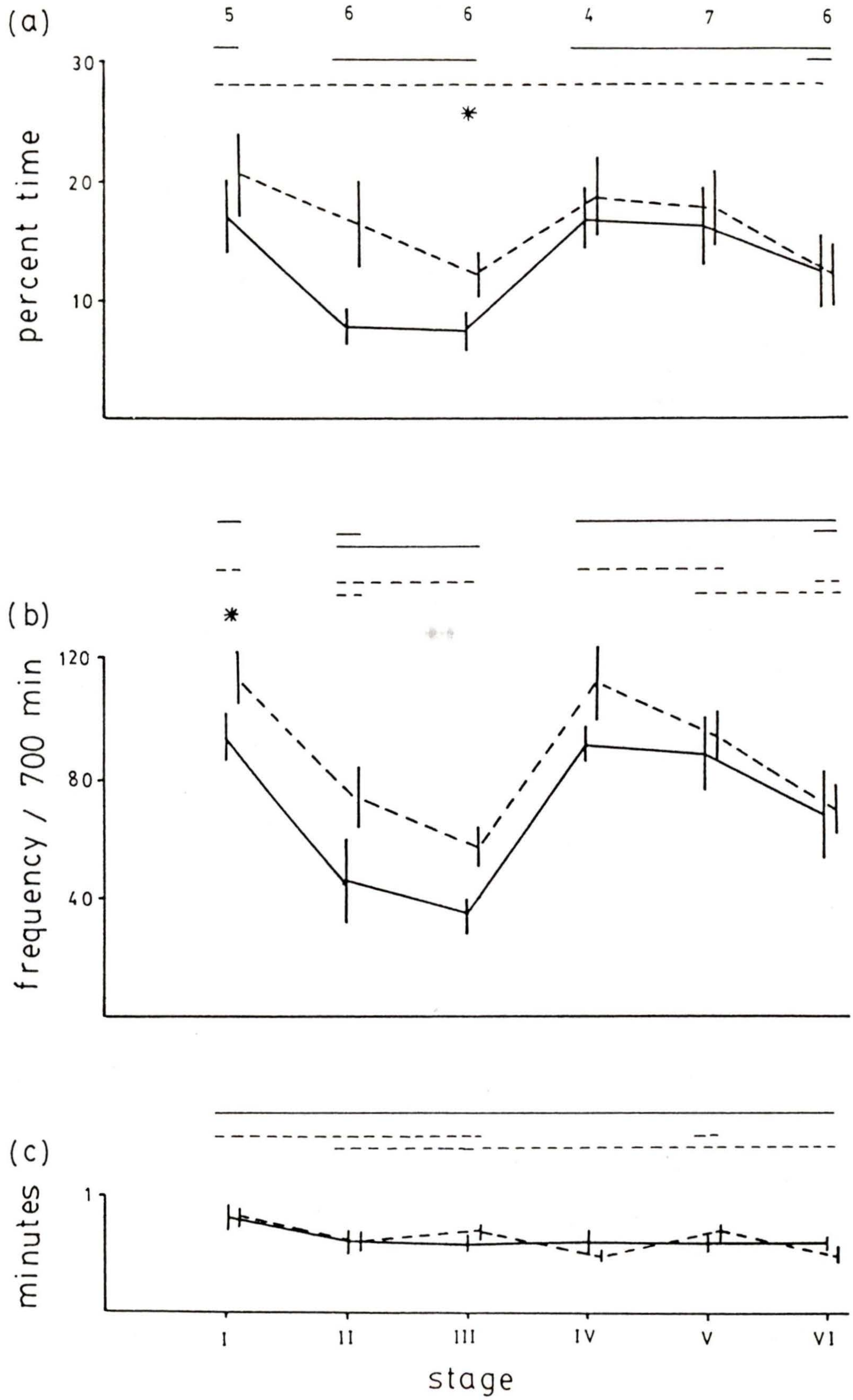
(b) frequency / 700 min of STBU

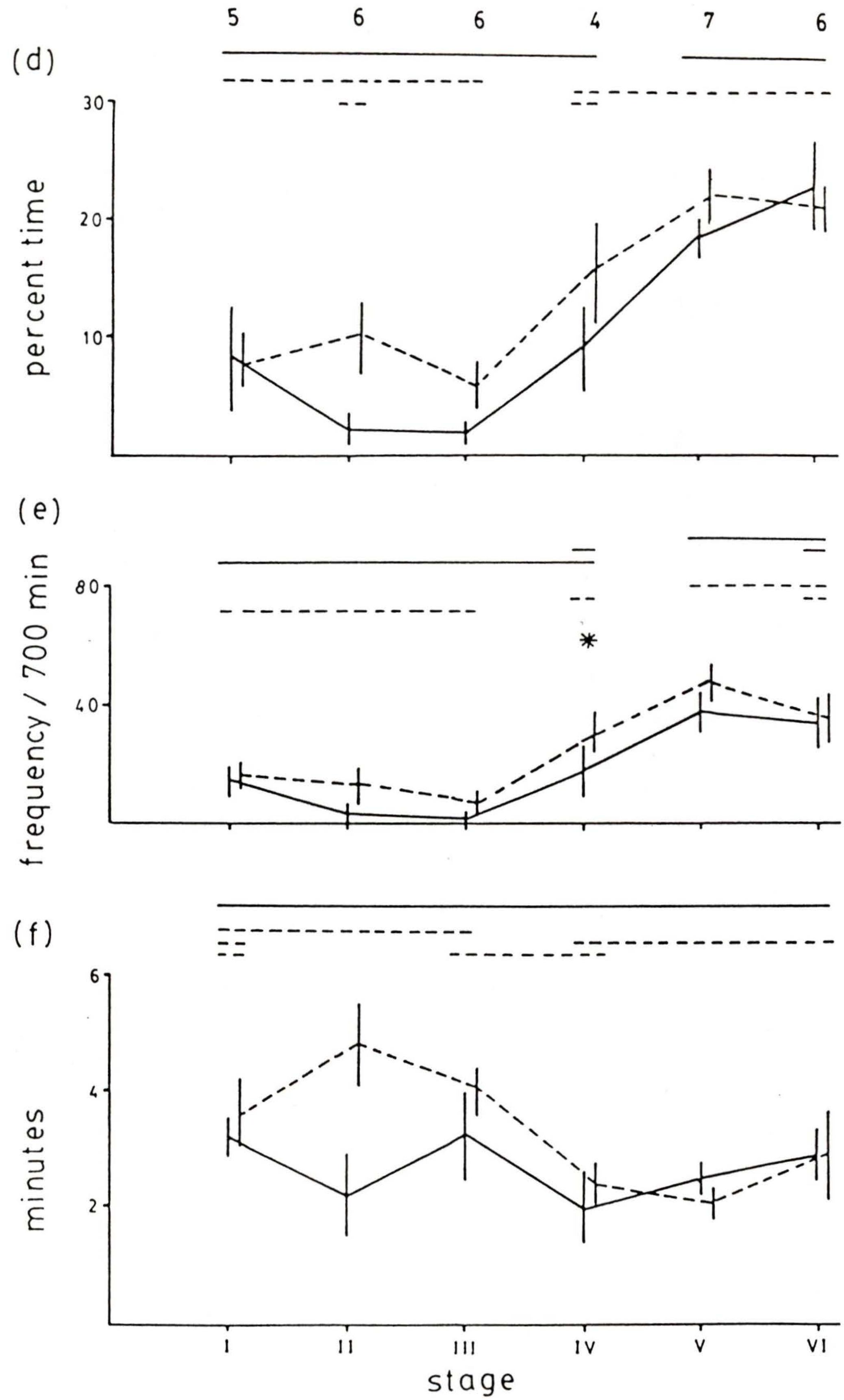
(c) median bout duration of STBU

(d) percentage of time spent STBOB

(e) frequency / 700 min of STBOB

(f) median bout duration of STBOB.


(a)
5
6
6
4
7
6
30
20
10
percent time
(b)
120
80
40
frequency / 700 min
(c)
1
minutes
I
II
III
IV
V
VI
stage


5
6
6
4
7
6
(d)
percent time
30
20
10
(e)
frequency / 700 min
80
40
(f)
minutes
6
4
2
I
II
III
IV
V
VI
stage

followed by an increase after hatching, was due mainly to the amount of time spent STBOB (Fig. 8a, d). Females differed from males in that they significantly reduced the amount of time they spent STBU during incubation, which was followed by a significant increase once the chicks hatched (Fig. 8a). Both sexes maintained similar low percentages of time STBOB until hatching, when they both significantly increased the amount of time spent STBOB (Fig. 8d). However, males spent more time than females did STBOB during incubation (Fig. 8d). This was primarily because males engaged in a greater number of long bouts of this behaviour and thus differed significantly from females (Fig. 9).

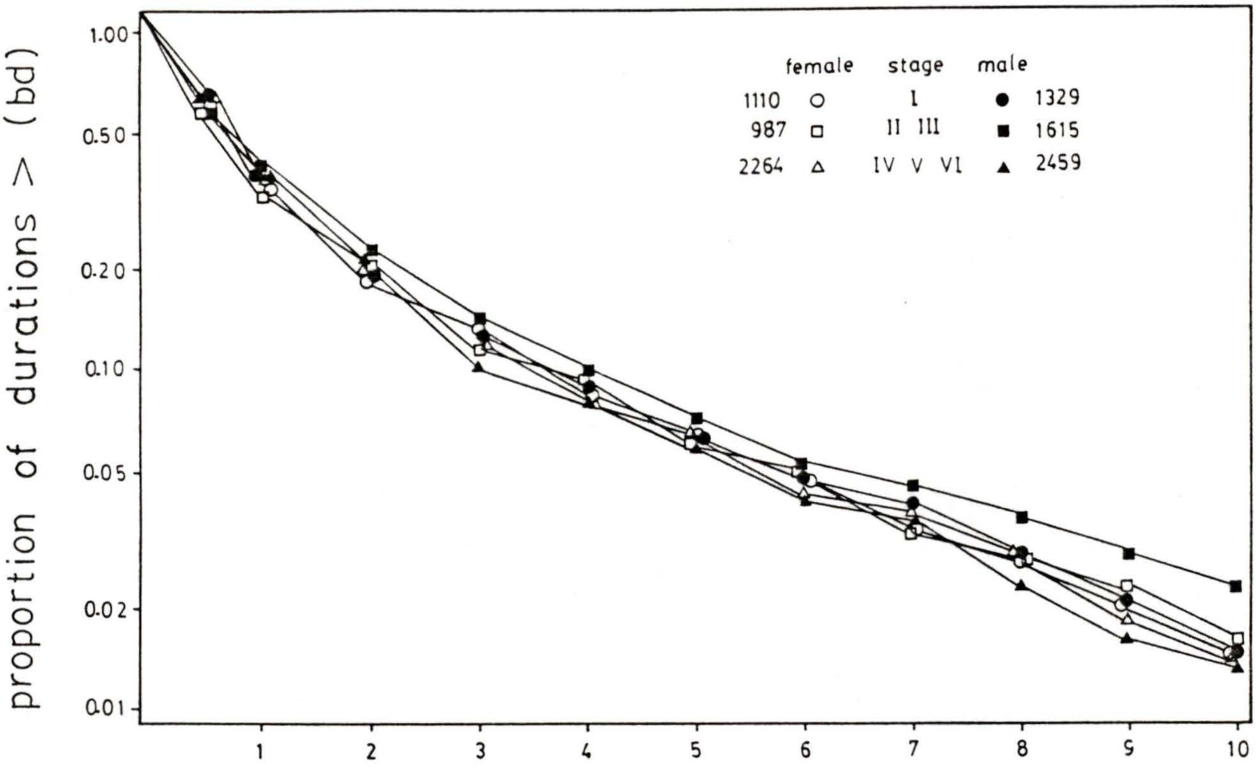
Once eggs hatched, bouts of STBOB for both male and female oystercatchers were briefer than they had been previously, and the birds were considered to be more alert (males' STBOB bouts were significantly shorter $D=17.4$ d.f.$=1$ $P<.01$; Fig. 9b). STBU bout lengths seemed to be unaffected by stage of the breeding cycle (Fig. 9a).

Sit (SI)

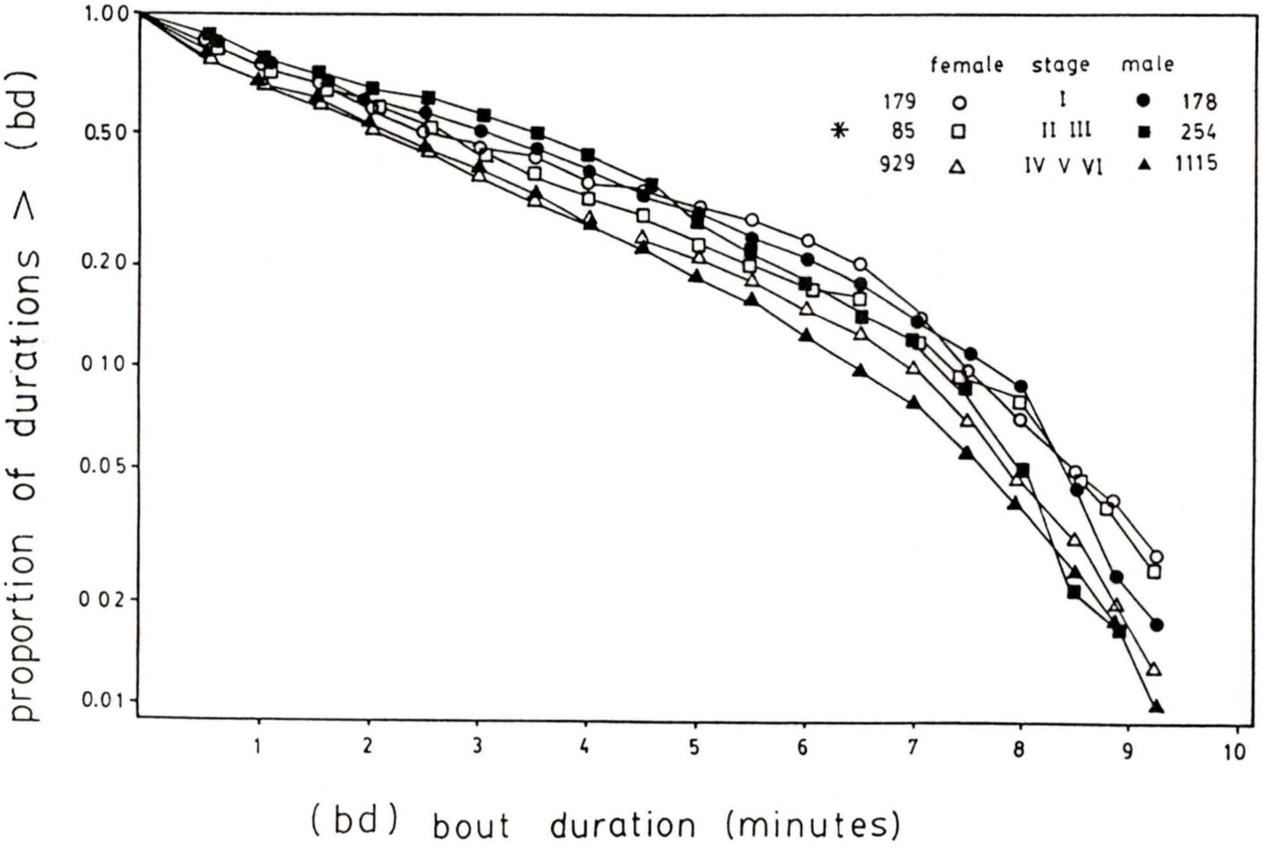
Male and female oystercatchers showed similar patterns in the percentage of time they spent sitting over the breeding season (Fig. 10). Both spent significantly more time sitting before and after incubation than while they

Figure 9: Comparison of frequency distributions of (a) STBU and (b) STBOB bout durations of male and female oystercatchers. Significant Lee-Desu values for intersexual comparisons within stages are indicated (*). Numbers in the symbol legend indicate the number of bouts included in the sample.

(a)


female
stage
male
1110 ○ I ● 1329
987 □ II III ■ 1615
2264 △ IV V VI ▲ 2459
proportion of durations > (bd)
1.00
0.50
0.20
0.10
0.05
0.02
0.01
1
2
3
4
5
6
7
8
9
10

(b)


female
stage
male
179 ○ I ● 178
* 85 □ II III ■ 254
929 △ IV V VI ▲ 1115
proportion of durations > (bd)
1.00
0.50
0.20
0.10
0.05
0.02
0.01
1
2
3
4
5
6
7
8
9
10
(bd) bout duration (minutes)

had eggs (Fig. 10). These trends were evident in both sitting postures, and were mainly due to the frequency with which birds engaged in these behaviours, although changes in bout lengths also contributed to the differences (Fig. 11 a-f). However, females tended to sit for longer bouts than did males (Fig. 11c, f). After hatching, both sexes increased the amount of time sitting. After the chicks were ten days old, females tended to spend more time sitting than their mates did, but the difference was not significant (Fig. 11a-f). This post-hatch increase was due primarily to the amount of time spent SIBOB which increased beyond prenesting levels (Fig. 11a-f).

Oystercatchers without eggs or chicks tended to sit for bouts that were longer than during other stages (SIBU 22% > 5 minutes during prenesting vs. 10% > 5 minutes during chick rearing; SIBOB 60% > 10 minutes during prenesting vs. 40% > 10 minutes during early chick rearing stages; Fig. 12). Oystercatchers with unfledged chicks tended to have shorter SIBOB bouts than they did after the chicks could fly, when their sitting bout durations became similar to those during Stage I (Fig. 12b). Finally, males and females tended to engage in bouts of similar duration, although before egg laying, SIBOB bouts by females tended to be longer (Fig. 12b). These observations suggest that oystercatchers with newly hatched chicks were more alert than oystercatchers in other stages and males were more

Figure 10: Comparison of percentage of time spent in SI by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. None of the paired t-test values for intersexual comparisons within stages were significant. Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

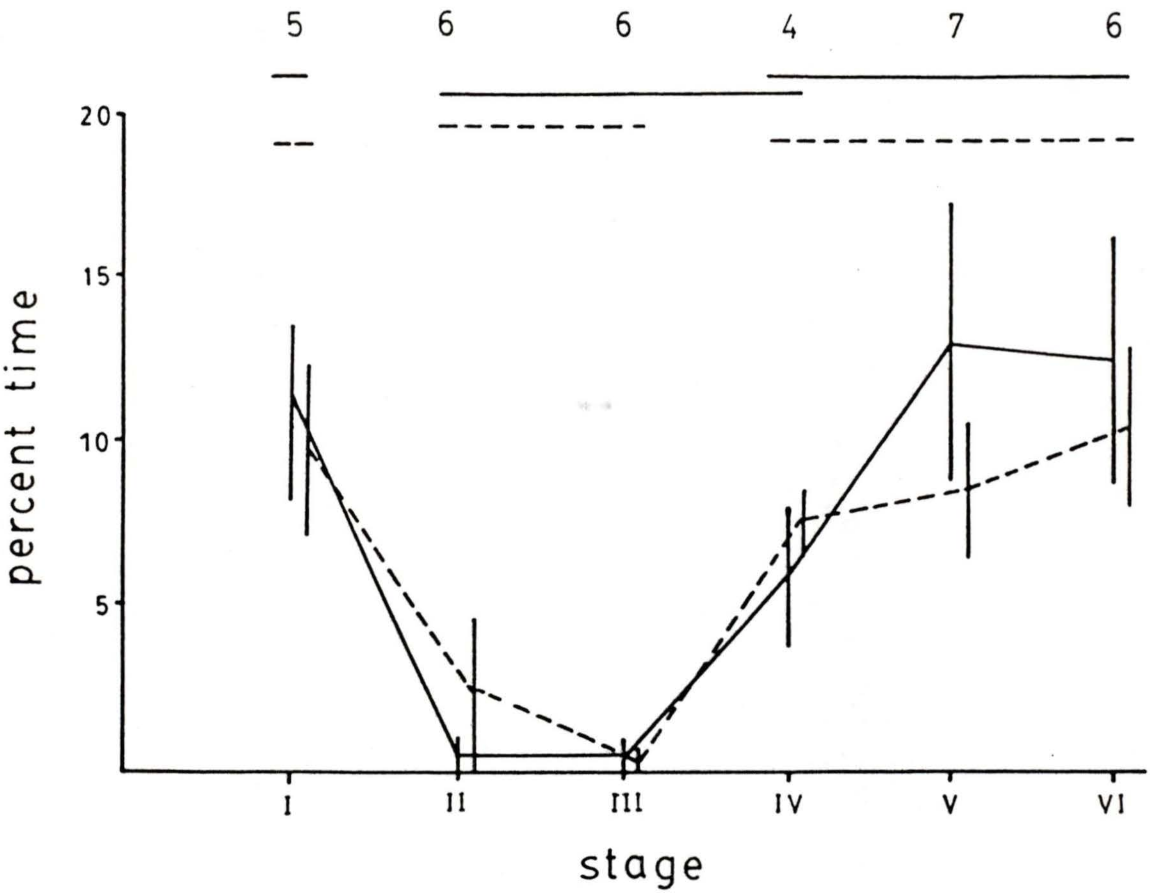

5
6
6
4
7
6
20
15
10
5
percent time
I
II
III
IV
V
VI
stage

Figure 11: Comparison of percentage of time, frequency and median bout duration of SIBU and SIBOB by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. None of the paired t-test values for intersexual comparisons were significant. Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

(a) percentage of time spent SIBU

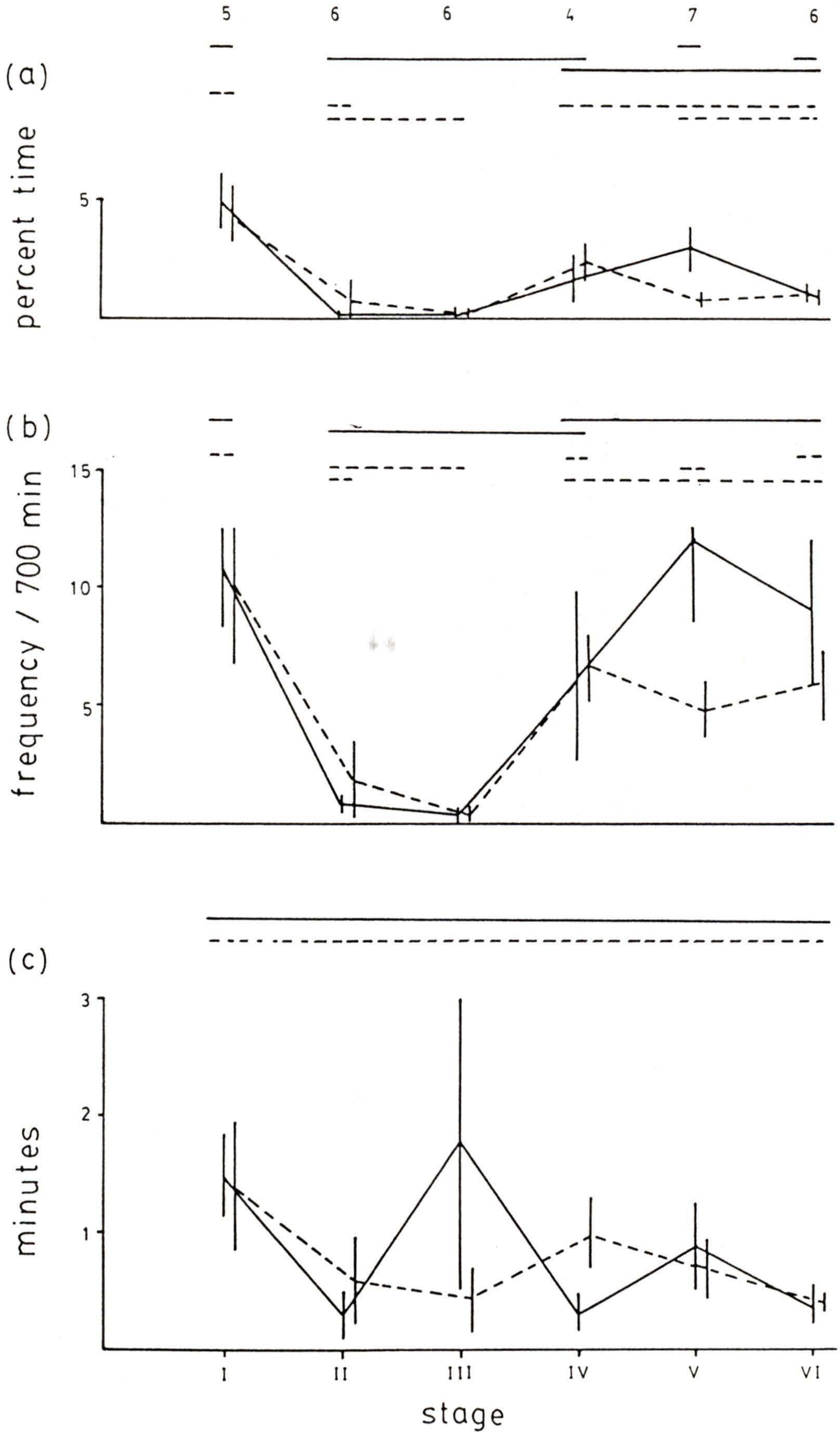
(b) frequency / 700 min of SIBU

(c) median bout duration of SIBU

(d) percentage of time spent SIBOB

(e) frequency / 700 min of SIBOB

(f) median bout duration of SIBOB.


5
6
6
4
7
6
(a)
percent time
5
(b)
frequency / 700 min
15
10
5
(c)
minutes
3
2
1
I
II
III
IV
V
VI
stage

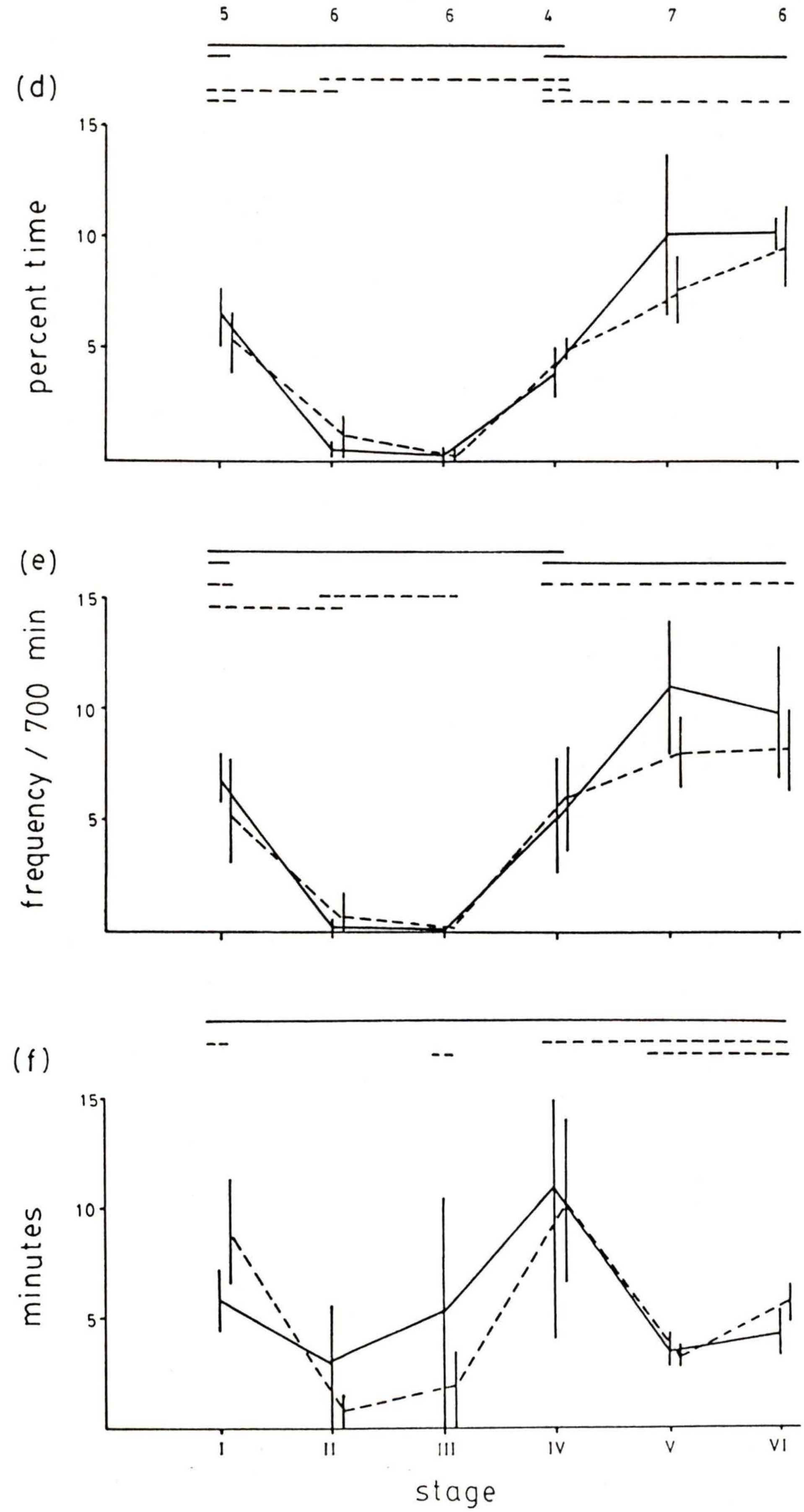
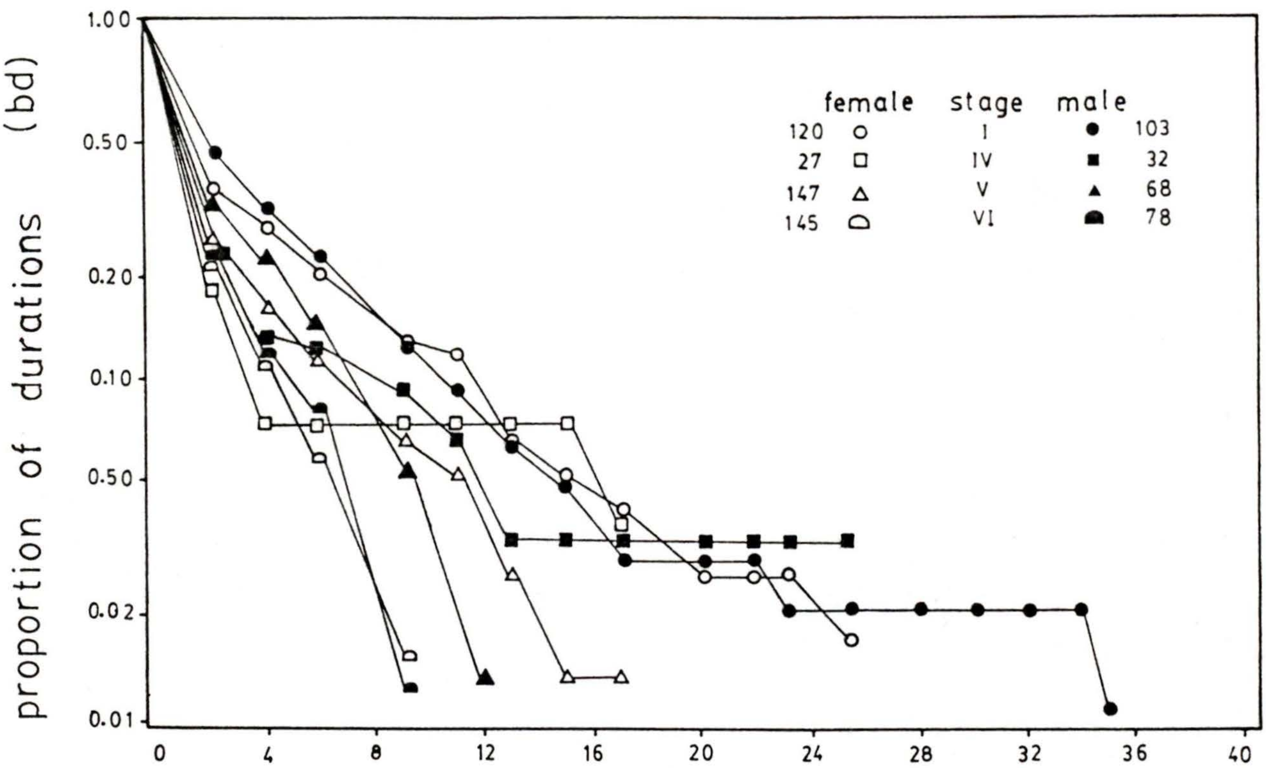
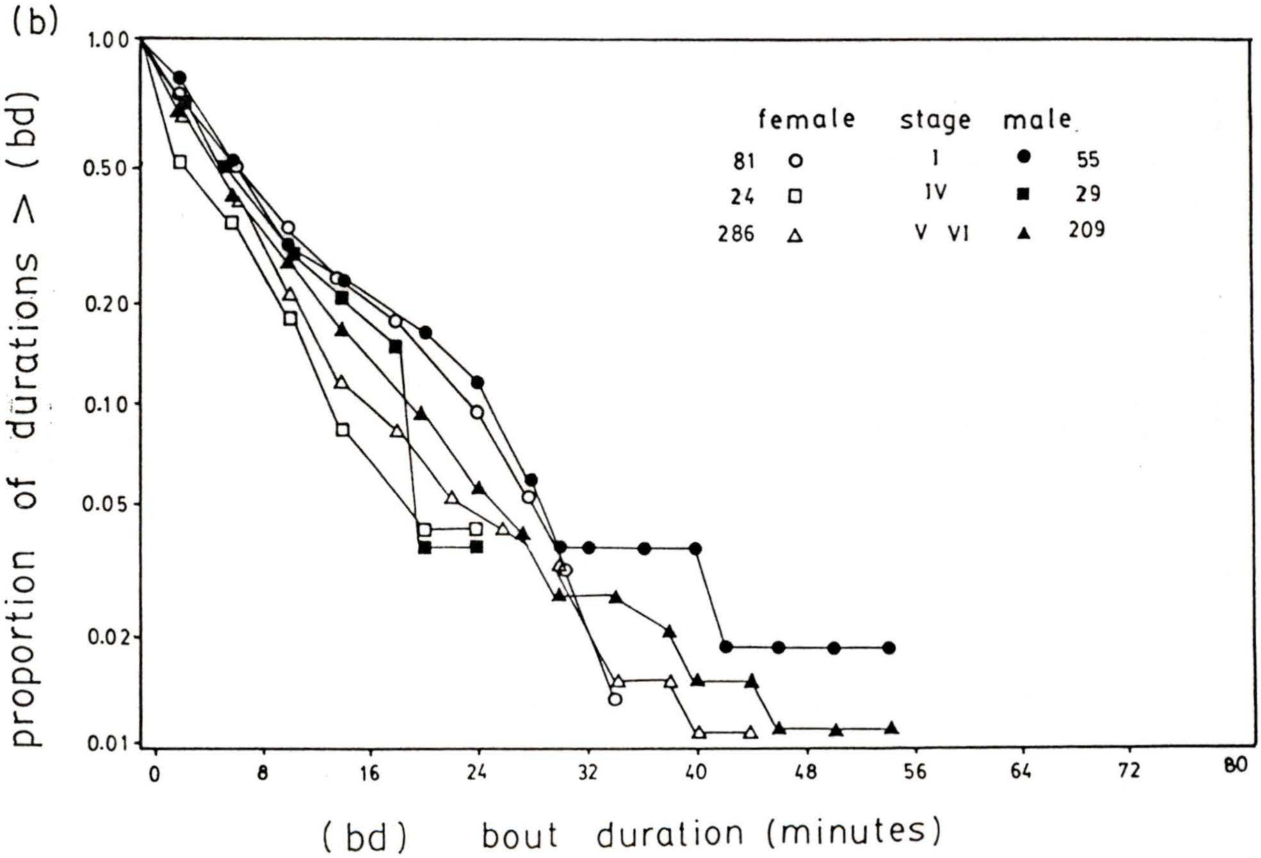

5
6
6
4
7
6
(d)
15
10
5
percent time
(e)
15
10
5
frequency / 700 min
(f)
15
10
5
minutes
I
II
III
IV
V
VI
stage

Figure 12: Comparison of frequency distributions of (a) SIBU and (b) SIBOB bout duration of male and female oystercatchers. None of the Lee-Desu values for intersexual comparisons within stages were significant. Numbers in symbol legend indicate the number of bouts included in the sample.

(a)


proportion of durations (bd)
female stage male
120 I 103
27 IV 32
147 V 68
145 VI 78
1.00
0.50
0.20
0.10
0.50
0.02
0.01
0
4
8
12
16
20
24
28
32
36
40

(b)


proportion of durations > (bd)
female stage male
81 I 55
24 IV 29
286 V VI 209
1.00
0.50
0.20
0.10
0.05
0.02
0.01
0
8
16
24
32
40
48
56
64
72
80
(bd) bout duration (minutes)

alert than females prior to egg laying.

Preen (PR)

As seen in other behaviours, the stage of the breeding cycle significantly influenced preening (Fig 13a-c). Incubating oystercatchers preened less than they did before and after nesting (Fig. 13a-c). Oystercatchers with young chicks also did not preen as much as oystercatchers without eggs or chicks and the amount of time spent preening increased as the chicks grew older (Fig. 13a-c).

Males spent slightly more time preening than their mates did during most stages but there was variability among pairs and these differences were not significant (Fig. 13a).

Oystercatchers with chicks tended to have shorter preening bouts than oystercatchers did in preceding stages but the sexes were similar (Fig. 14). Males with eggs tended to preen in shorter bouts than females did and this difference was significant (Fig. 14). Oystercatchers without eggs or chicks tended to have the longest preening bouts but there was no difference between males and females (Fig. 14).

As with other behaviours, the brevity of a preening bout may reflect alertness, so the higher percentage of short

Figure 13: Comparison of (a) percentage of time, (b) frequency and (c) median bout duration of PR by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. None of the paired t-test values for intersexual comparisons were significant. Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

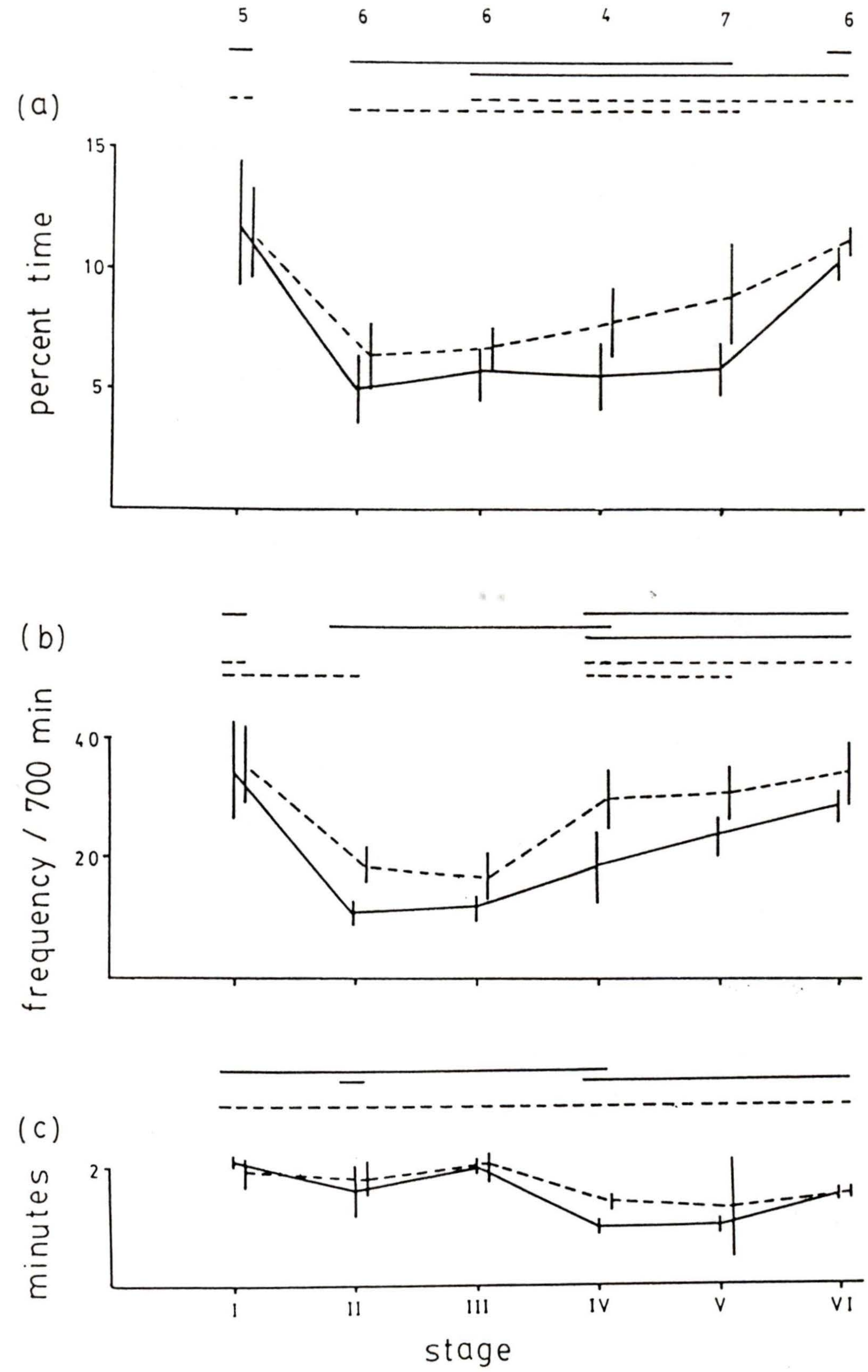
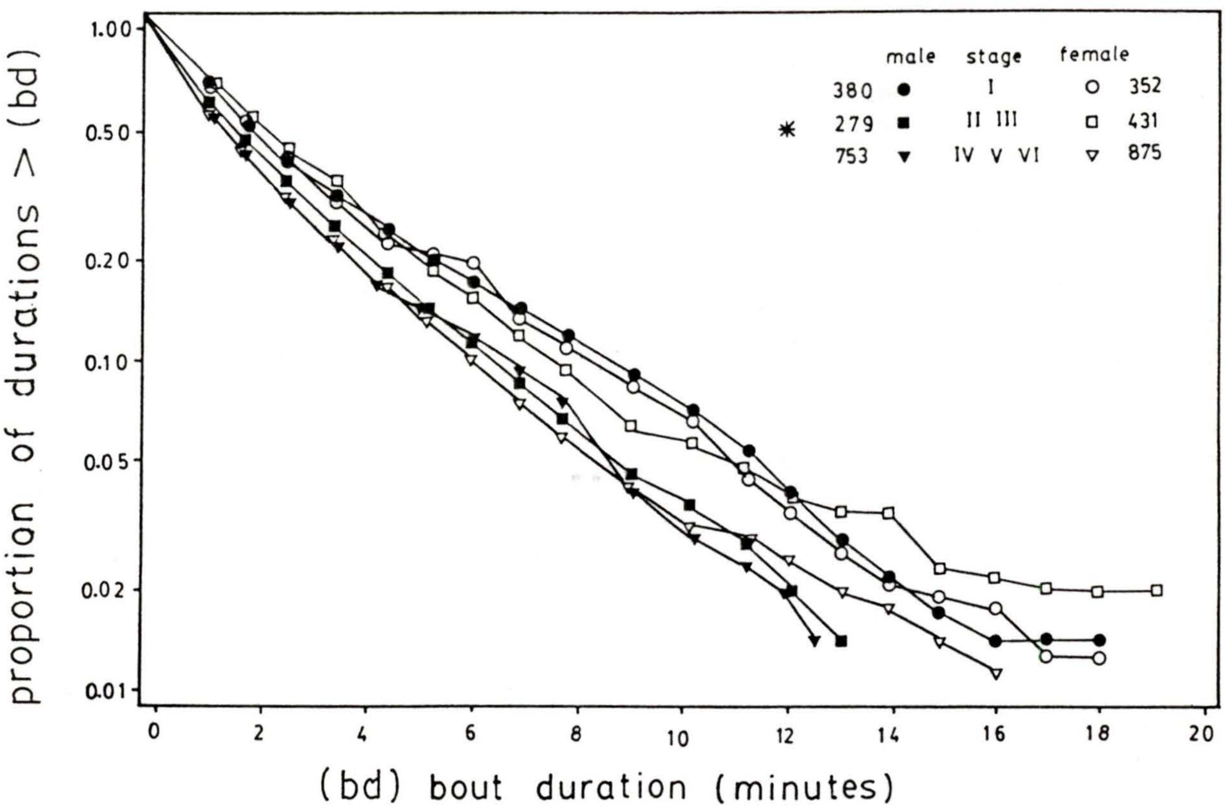

5
6
6
4
7
6
(a)
percent time
15
10
5
(b)
frequency / 700 min
40
20
(c)
minutes
2
I
II
III
IV
V
VI
stage

Figure 14: Comparison of frequency distributions of PR bout durations of male and female oystercatchers. Significant Lee-Desu values for intersexual comparisons are indicated (*). Numbers in symbol legend indicate the number of bouts included in the sample.



proportion of durations > (bd)
1.00
0.50
0.20
0.10
0.05
0.02
0.01
male
stage
female
380
I
352
*
279
II III
431
753
IV V VI
875
0
2
4
6
8
10
12
14
16
18
20
(bd) bout duration (minutes)

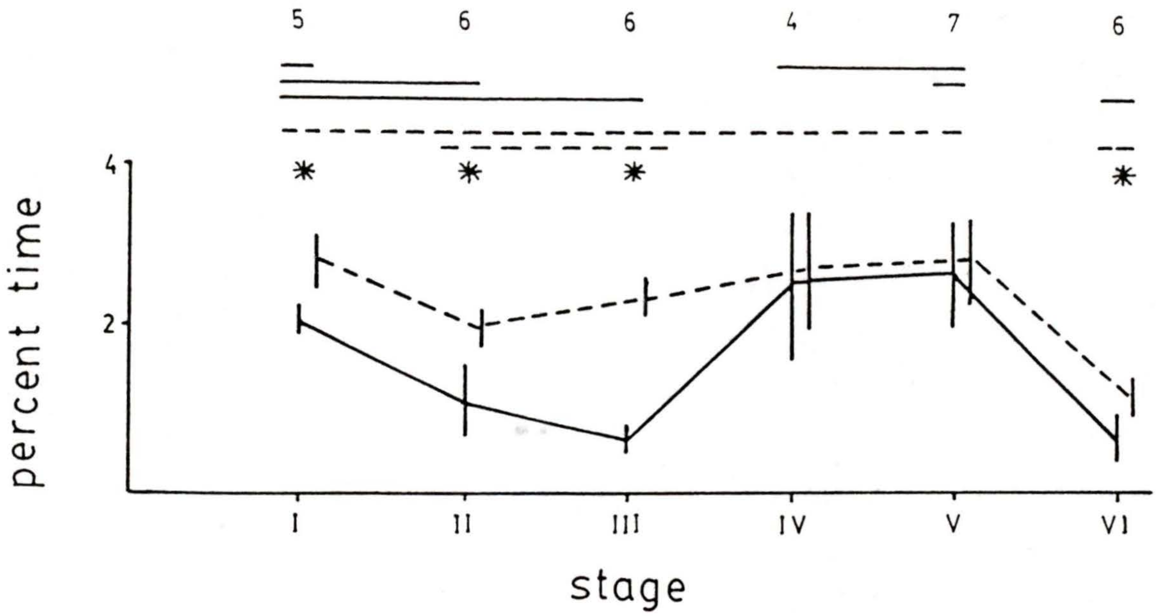
preening bouts by males during incubation suggests that they were more alert than females. Similarly, oystercatchers were more alert with chicks than during stages with eggs or before eggs were laid.

Agonistic (*AG*)

Males spent more time in agonistic behaviours (HU and PIPE) than females and were thus considered to be more aggressive during most stages of the breeding season (Fig. 15). After Stage I, males maintained similar levels of aggression over the following stages until the chicks fledged (Stage VI). Incubating females were less aggressive than they had been prior to egg laying, but they became as aggressive as males after the chicks hatched. Females were also less aggressive after their chicks could fly.

Closer examination showed that the sexes differed in the type of aggression engaged in (inter- or intraspecific), and the type was also influenced by the stage of the breeding season. Generally, during prenesting and incubation stages (Stage I - III), both sexes directed their aggression toward conspecifics. After hatching (Stage IV), both sexes, but particularly females, became more aggressive toward gulls.

Figure 15: Comparison of the percentage of time spent in AG by male (----) and female (——) oystercatchers. Significant paired t-test values are indicated (*). Vertical bars represent ± standard error. Means joined by horizontal lines on the same level are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.


5
6
6
4
7
6
4
2
percent time
I
II
III
IV
V
VI
stage

Intraspecific interactions (PIPE)

Oystercatchers piped with their mates and with intruding conspecifics. Piping interactions with mates constituted approximately 25 per cent (±13.4 s.d.; n=42) of the interactions with conspecifics and there were no differences among the stages or between sexes in the percentage these interactions made up of the total.

Territorial intrusions by conspecifics (conspecifics on the ground and piping parties flying overhead) occurred at a fairly constant rate over the breeding season at about 18 intrusions in 700 minutes (±6.1 s.d.; n=21). Males responded aggressively toward intruders more often than did females, and consequently spent more time piping during all stages (Fig. 18, 19a). However, the response rate changed over the six stages and females and males responded differently to intrusions over the breeding season. Females with eggs and young chicks did not respond to as many intrusions as they did before eggs were laid and after fledging (Fig. 17a). In contrast, males responded to most intrusions regardless of nesting stage (Fig. 17a). This pattern was also reflected in the percentage of time the oystercatchers spent piping (Fig. 16).

This pattern of response by the sexes over the breeding season appeared to be due mainly to the response to piping parties, although females also did not respond to as many

Figure 16: Comparison of percentage time in PIPE by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. Significant paired t-test values for intersexual comparisons within stages are indicated (*). Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

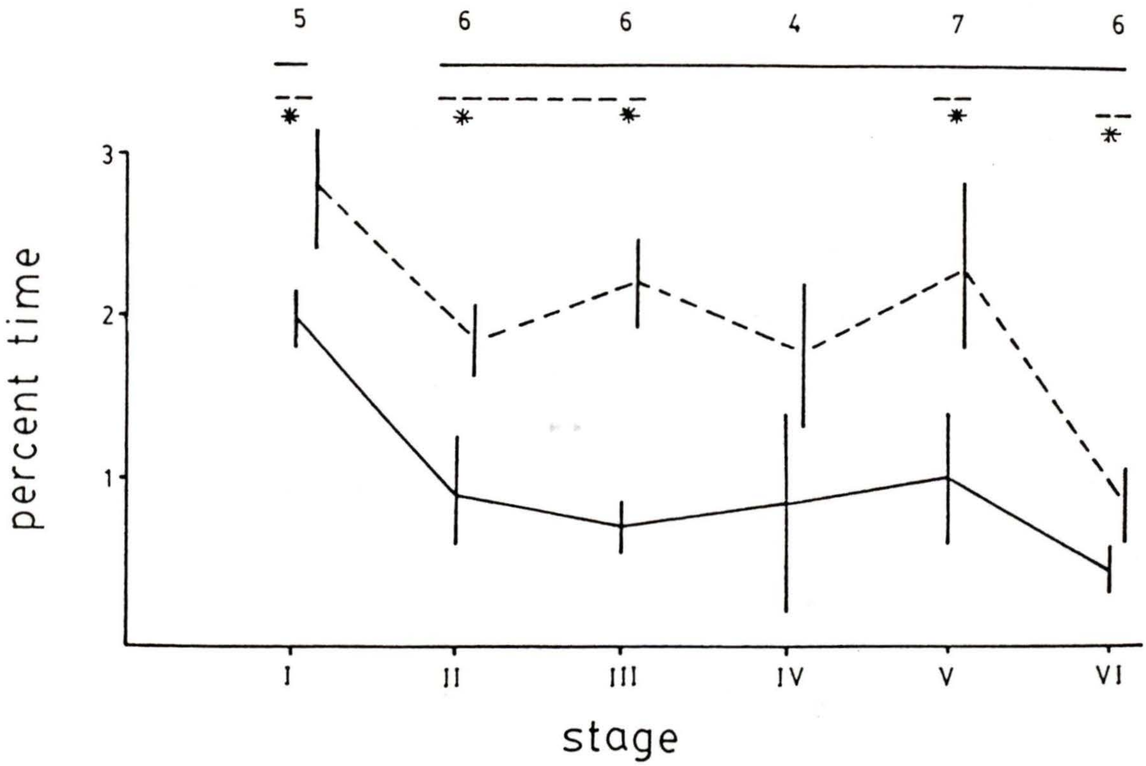

5
6
6
4
7
6
3
2
1
percent time
I
II
III
IV
V
VI
stage

Figure 17: Comparison of the percentage of intrusions by conspecific responded to by male (----) and female (——) oystercatcher. Vertical bars represent ± range. Number of individuals included in the samples are indicated at the top.

(a) all intrusions by conspecifics

(b) conspecifics flying overhead (piping parties)

(c) conspecifics landing on the territory

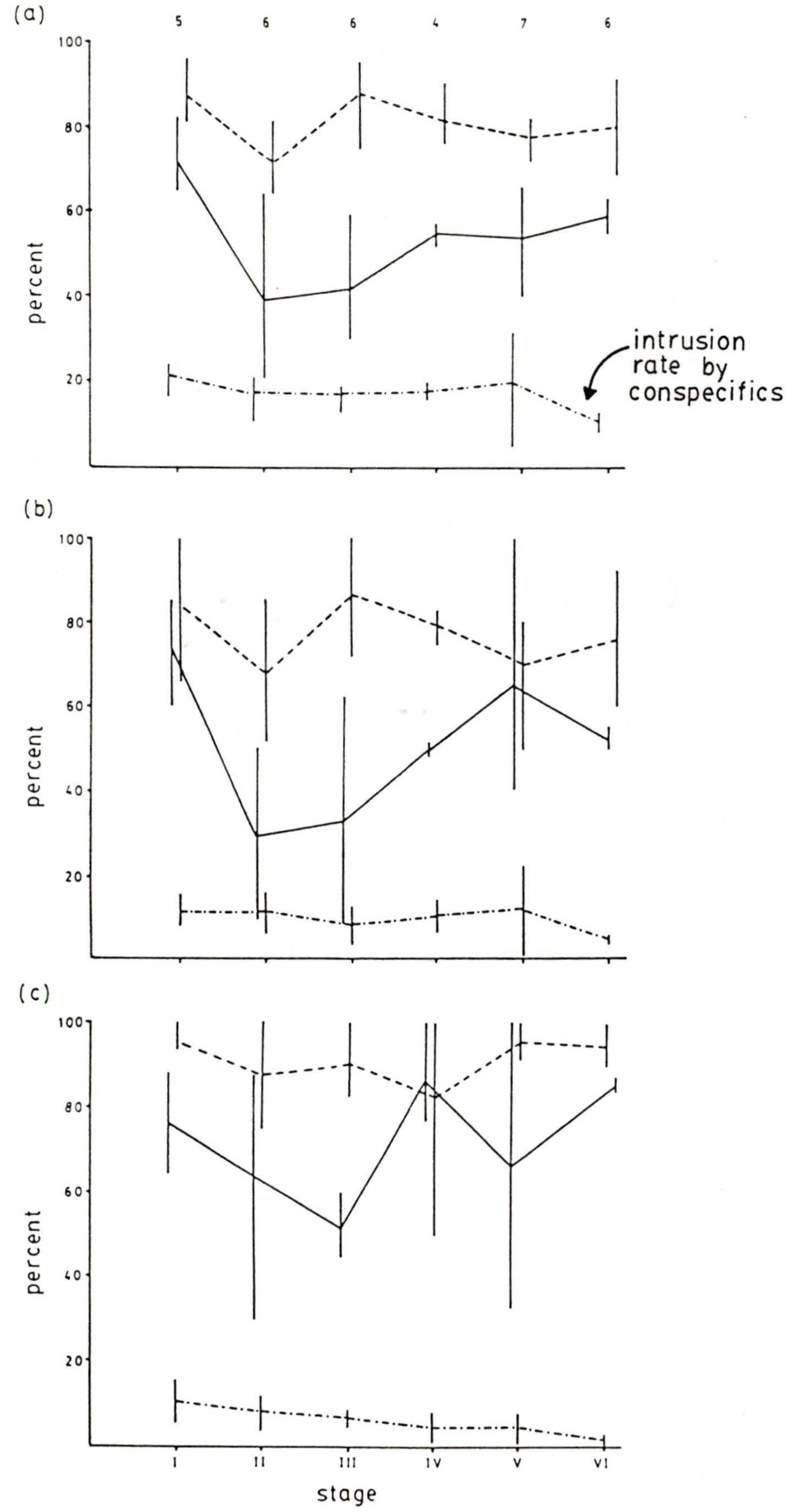

(a)
5
6
6
4
7
6
100
80
60
40
20
percent
intrusion rate by conspecifics
(b)
100
80
60
40
20
percent
(c)
100
80
60
40
20
percent
I
II
III
IV
V
VI
stage

Figure 18: Comparison of the percentage of time spent in HU by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. Significant paired t-test values for intersexual comparisons are indicated (*). Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

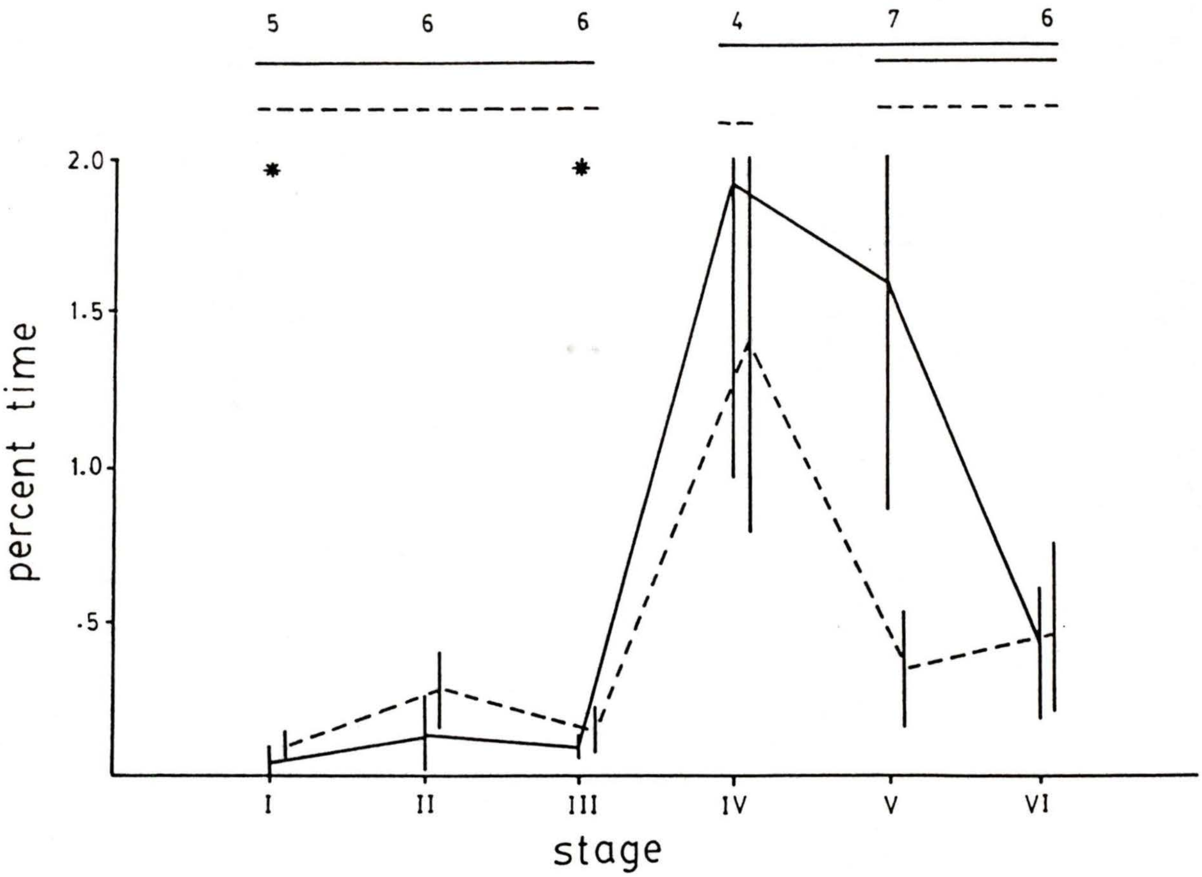

5
6
6
4
7
6
*
*
2.0
1.5
1.0
.5
percent time
I
II
III
IV
V
VI
stage

Figure 19: Comparison of the percentage of time, frequency and median bout duration of HUG and HUA by male (----) and female (——) oystercatchers. Vertical bars represent ± standard error. Significant paired t-test values for intersexual comparisons are indicated (*). Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

(a) percentage of time spent HUG

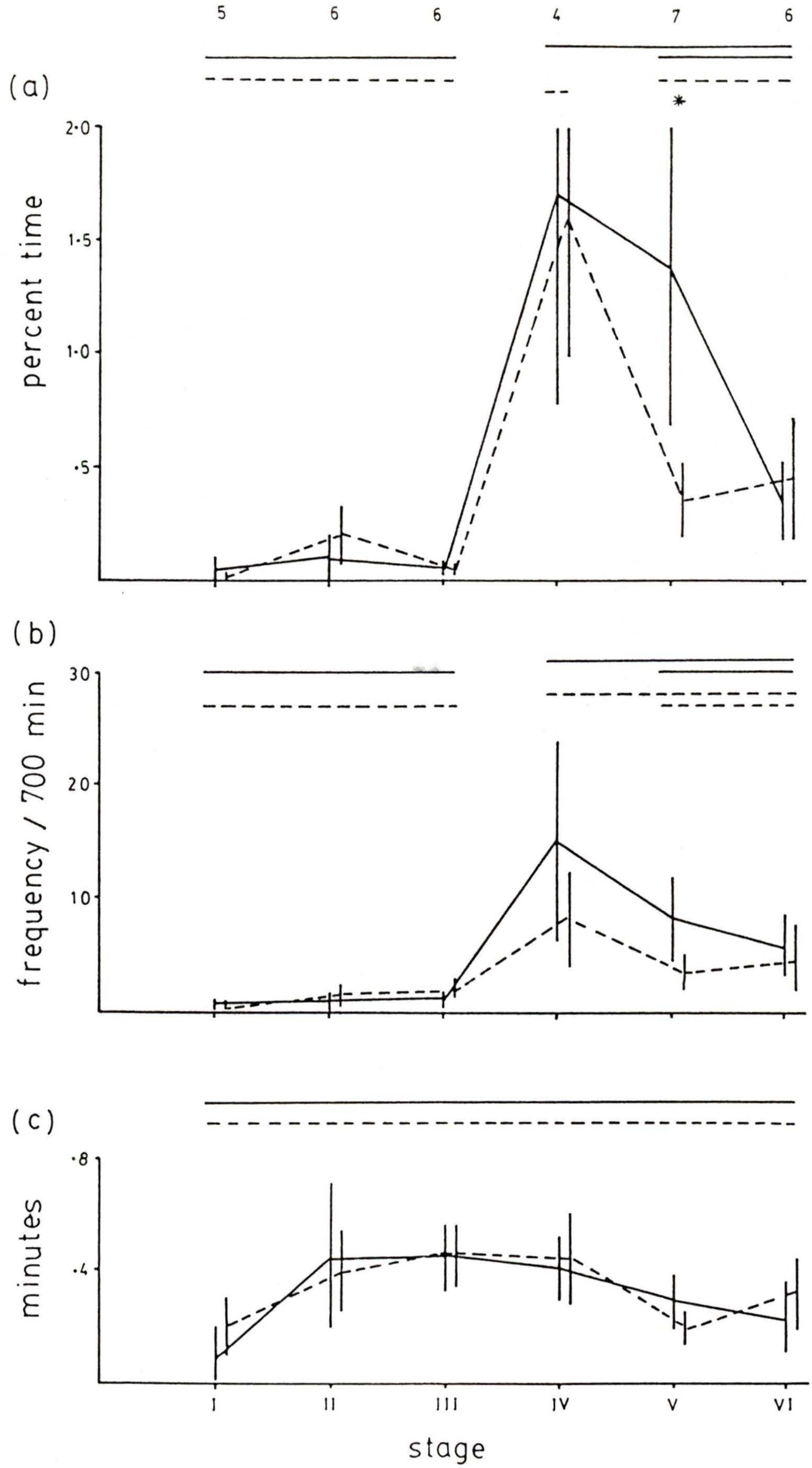
(b) frequency / 700 min of HUG

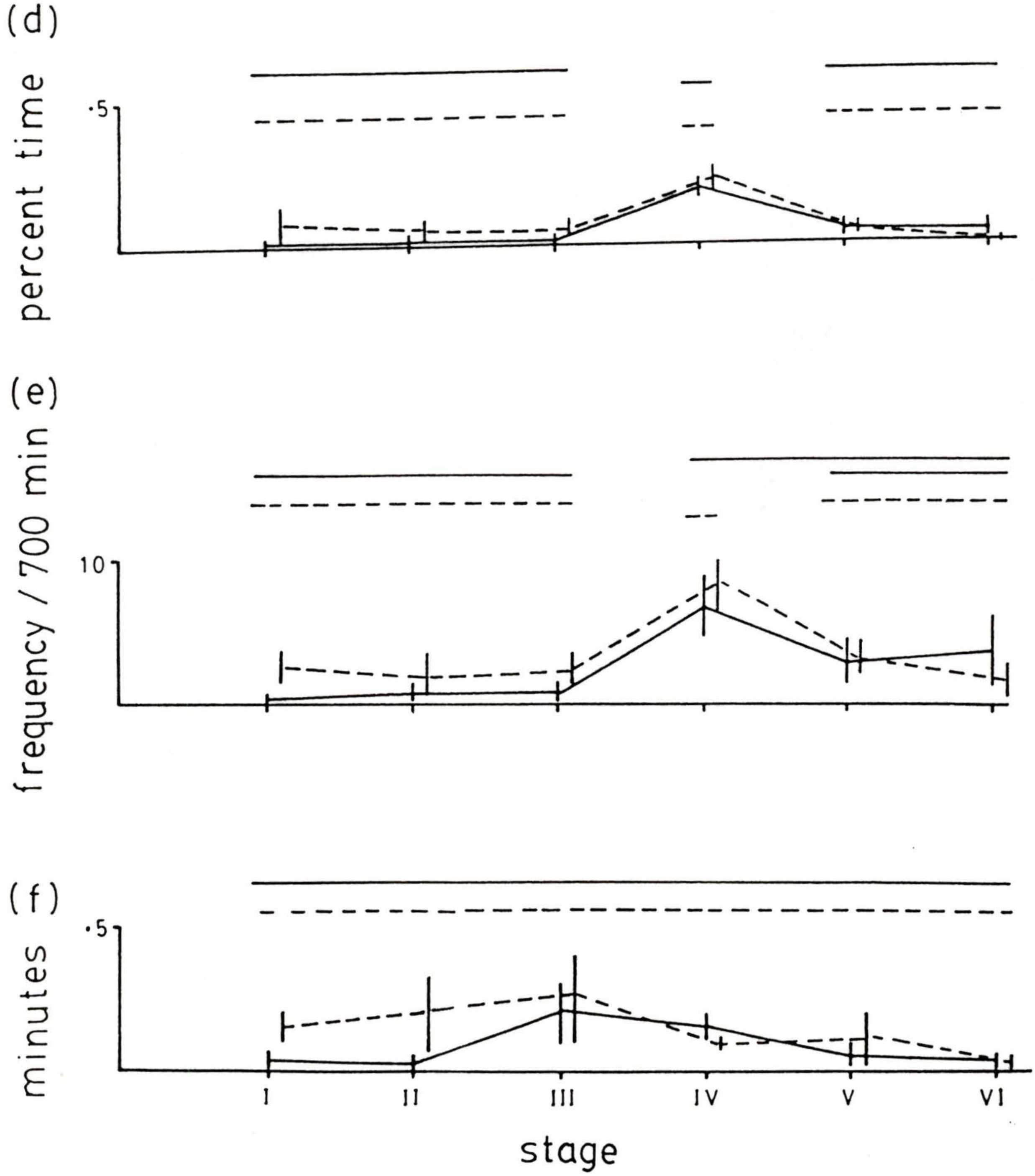
(c) median bout duration of HUG

(d) percentage of time spent HUA

(e) frequency / 700 min of HUA

(f) median bout duration of HUA.


5
6
6
4
7
6
(a)
*
2·0
1·5
1·0
·5
percent time
(b)
30
20
10
frequency / 700 min
(c)
·8
·4
minutes
I
II
III
IV
V
VI
stage


(d)
percent time
·5
(e)
frequency / 700 min
10
(f)
minutes
·5
I
II
III
IV
V
VI
stage

conspecifics that landed on the territory (Fig. 17a-c).

Attacks on intruding conspecifics were brief (< 1 minute) and accounted for less than .05 per cent of the time budget of females and less than .10 per cent of that of males. Males attacked intruding conspecifics more frequently (82% of 225) than females did (18% of 225). Most attacks by males (77% of 184) occurred in the early part of the breeding cycle, prior to hatching, while attacks by females were independent of stage (51% of 41 before hatching).

Interspecific interactions (HU)

The stage of the breeding season had a significant influence on the level of aggression exhibited toward potential predators, and males and females differed in their response to these species (Fig. 18). Before hatching, males spent more time exhibiting aggressive HU behaviours than did females, primarily because males attacked gulls more frequently (Fig. 18, 19a-f). After hatching, oystercatchers significantly increased their aggressiveness toward gulls; this was followed by a gradual decrease toward fledging (Fig. 20).

Parental Care (PC)

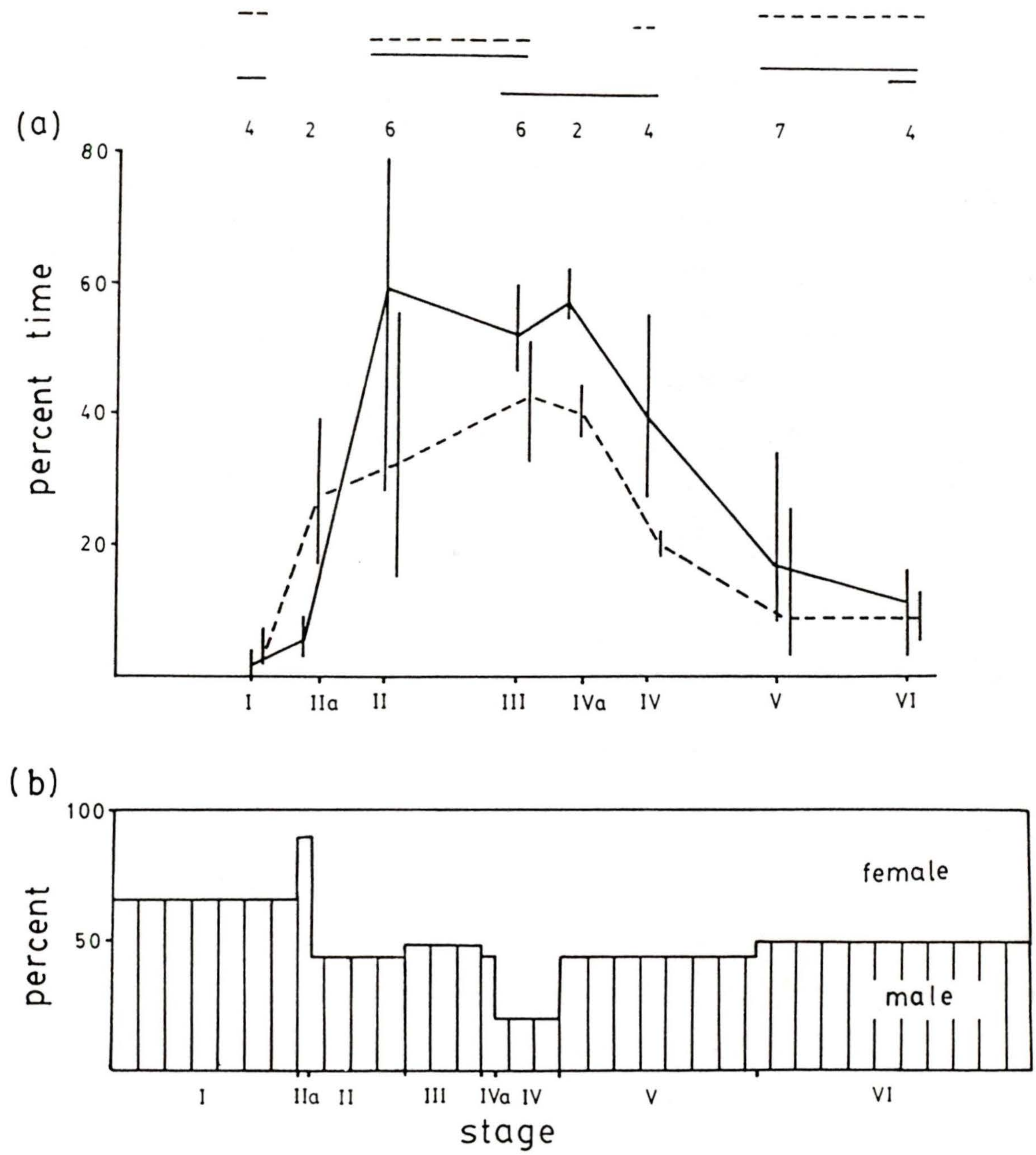
The sexes differed in the amount of time spent in parental care during each stage of the breeding season (Fig. 20a). To clarify these differences, I examined the percentage contribution by each sex, in addition to the the percentage of time spent in these behaviours. Males contributed more toward parental duties before clutch completion, particularly during egg laying, when males did 90 per cent of the egg covering. After clutch completion (Stage II), females incubated slightly more than males; the sexes shared the incubation duties almost equally during the latter half of incubation (Stage III). Females contributed 80 per cent of the parental care to young chicks (Stage IV), but males subsequently increased their contribution, and oystercatchers with older chicks (Stage V and VI) shared parental duties almost equally.

I emphasize that parental care here refers to active parental behaviours only, including nest building, incubating, brooding, feeding and foraging for the chick, and does not include associated behaviours such as guarding and aggression, which are considered separately.

Nest-build (NB)

NP (nest-press) accounted for less than 1 per cent of the time-activity budget of Black Oystercatchers (Appendix

Figure 20: Comparison of the (a) percentage of time spent in PC by male (----) and female (——) oystercatchers PC and (b) per cent contribution by each sex. Vertical bars represent ± range. Numbers of individuals included in the samples are indicated at the top.


(a)
4
2
6
6
2
4
7
4
80
60
40
20
percent time
I
IIa
II
III
IVa
IV
V
VI
(b)
100
50
percent
female
male
I
IIa
II
III
IVa
IV
V
VI
stage

3) and was therefore included with estimates of BT for this presentation. Males did most nest-building. Before eggs were laid, males spent almost twice as much time as females in nest construction (Fig. 21a). This was mainly because they engaged in BT more often than females did and, to a lesser extent, because they exhibited longer BT bouts than females (Fig. 21a-c, 22). Females also did not spend as much time as males did in NP (female $\bar{x}$=.1%±.1 s.d., male $\bar{x}$=.5%±.5 s.d.; n=5), again primarily because females did not NP as frequently as males (females $\bar{x}$=4.3±3.4 s.d., males $\bar{x}$=9.2±2.9 s.d.; n=5).

Females increased the amount of time they spent nest building when they began to lay eggs, until they reached a level similar to males in Stage IIa (Fig. 21a). This increase was mainly due to the increased length of BT bouts by females, which exceeded those of males (Fig. 21a-c, 22).

Males and females continued to exhibit similar but ever decreasing amounts of nest-building behaviour throughout incubation, and it usually occurred when a bird left the nest (Fig. 21 a-c).

Incubate (INC)

The range of participation in INC was variable; for females it was 1.1 per cent to 76.3 per cent of the total

Figure 21: Comparison of (a) percentage of time, (b) frequency and (c) median bout duration of BT by male (----) and female (——) oystercatchers. Significant paired t-test values are indicated (*). Vertical bars represent ± range. Numbers of individuals included in the samples are indicated at the top.

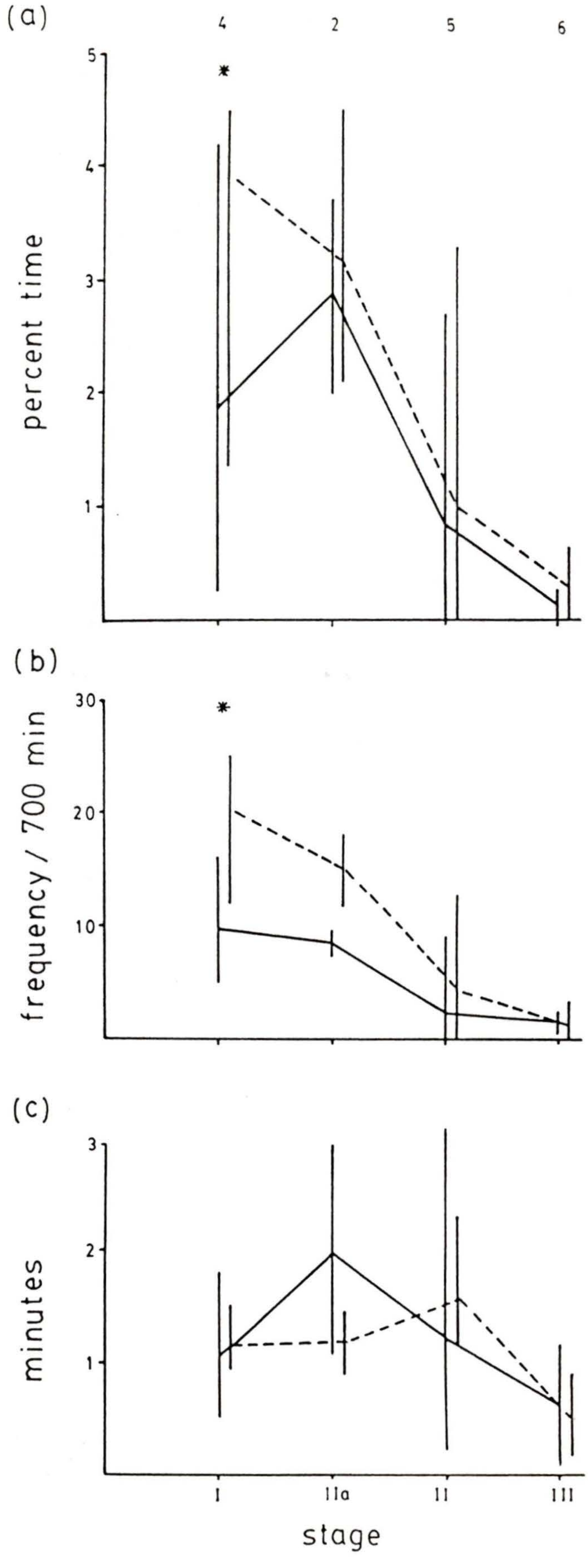
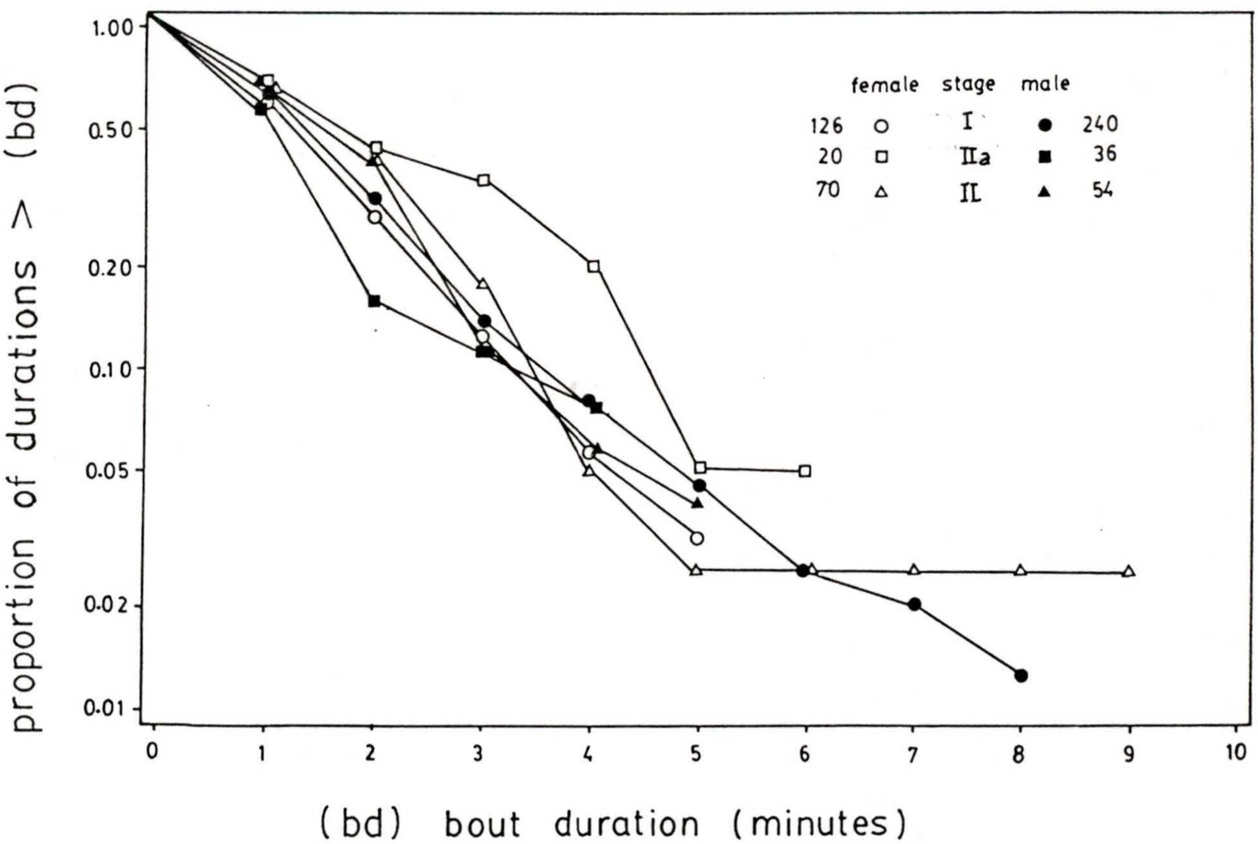

(a)
4
2
5
6
5
4
3
2
1
percent time
*
(b)
30
20
10
frequency / 700 min
*
(c)
3
2
1
minutes
I
IIa
II
III
stage

Figure 22: Comparison of frequency distributions of BT bout durations of male and female oystercatchers. None of the Lee-Desu values for intersexual comparisons within stages were significant. Numbers in the symbol legend indicate the number of bouts included in the sample.



proportion of durations > (bd)
1.00
0.50
0.20
0.10
0.05
0.02
0.01
0
1
2
3
4
5
6
7
8
9
10
(bd) bout duration (minutes)
female stage male
126 ○ I ● 240
20 □ IIa ■ 36
70 △ IL ▲ 54

observation time and for males it was 12.3 per cent to 54.8 per cent. Some of this variability among individuals of the same sex was due to variance among stages.

During egg laying (Stage IIa), the incomplete clutch was covered about 30 per cent of the time, mainly by the male (Fig. 23a). Incubation was sporadic and incubation bouts were short, particularly by females, with egg covering often lasting less than ten minutes (Fig. 23c, 24). Although not covered continuously, the egg was rarely left unguarded. It was often left uncovered for periods while the adult(s) stood close by, or when both adults infrequently left the nest area to pipe or forage. Males spent more time close to the nest than did females (Fig. 25). The proportion of time oystercatchers spend near (within 6 m) of the nest is important in defence of the nest-site, eggs and chicks. When parents are within this distance they can quickly confront potential predators.

After the last egg was laid, the clutch was incubated approximately 90 per cent of the time. The time off the nest was spent primarily in change-overs and in aggressive encounters with conspecifics. After clutch completion, males and females did not differ in the amount of time spent close to the nest but females took over most incubation duties (Fig. 25, 23a-c). However, the difference between the sexes in incubation attendance was

Figure 23: Comparison of the (a) percentage of time, (b) frequency and (c) median bout duration of INC by male (----) and female (——) oystercatchers. Significant paired t-test values for intersexual comparisons within Stage II and III are indicated (*). Vertical bars represent ± range. Numbers of individuals included in the samples are indicated at the top.

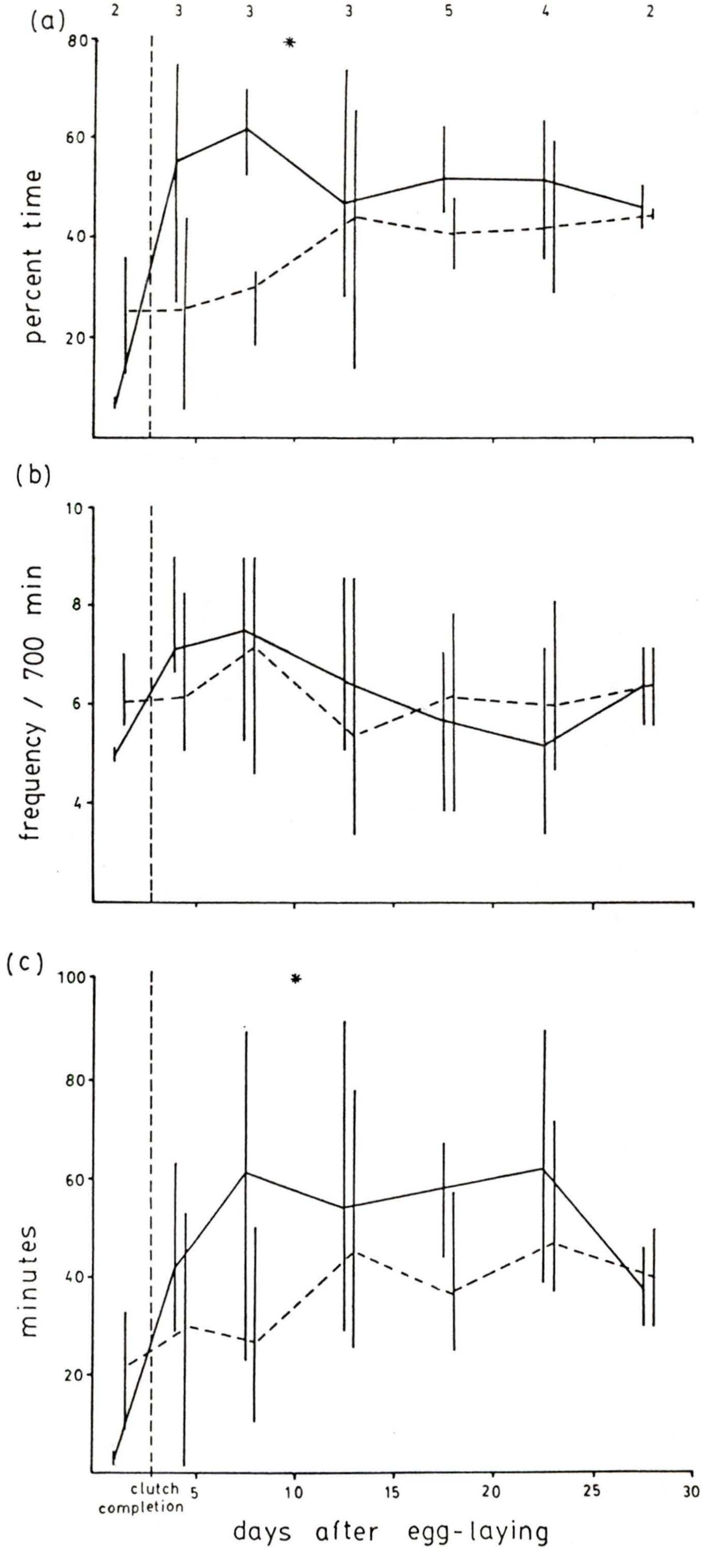

(a)
2 3 3 3 5 4 2
percent time
20
40
60
80
*
(b)
frequency / 700 min
4
6
8
10
(c)
minutes
20
40
60
80
100
*
clutch completion
5
10
15
20
25
30
days after egg-laying

Figure 24: Comparison of frequency distributions for bout durations of INC of male and female oystercatchers. Significant Lee-Desu values for intersexual comparisons within stages are indicated (*). Numbers in the symbol legend indicate the number of bouts included in the sample.

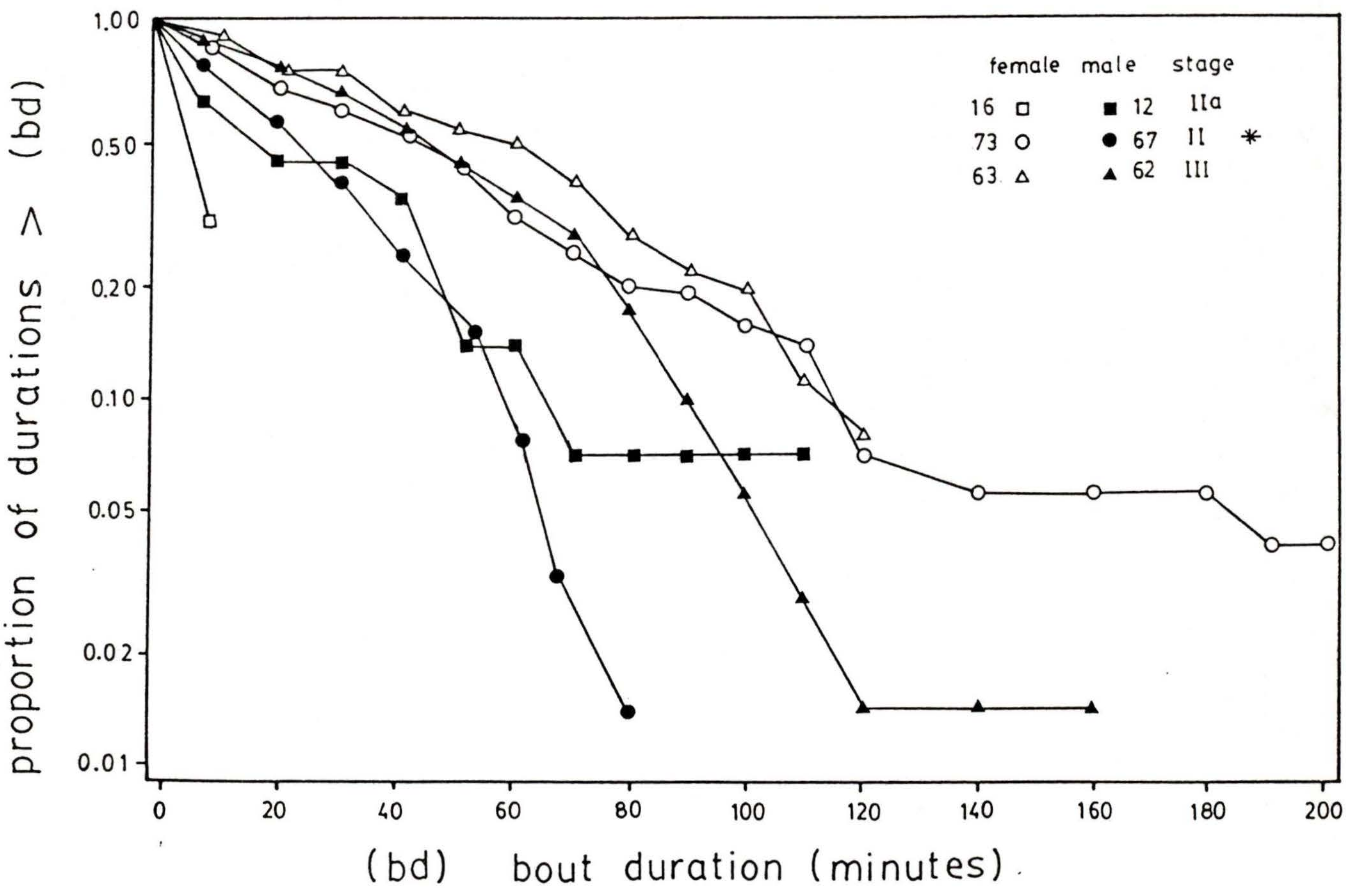
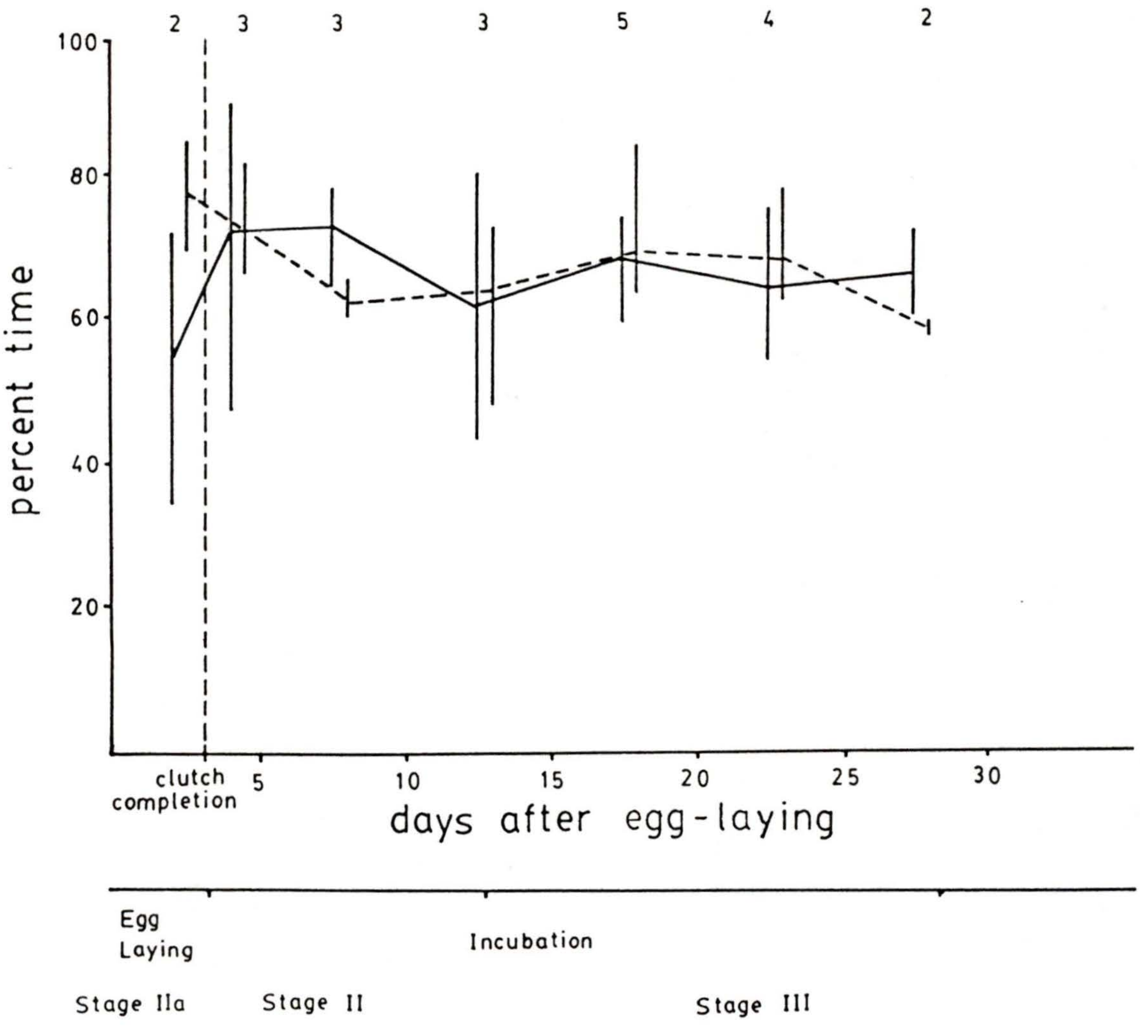

1.00
0.50
0.20
0.10
0.05
0.02
0.01
proportion of durations > (bd)
0
20
40
60
80
100
120
140
160
180
200
(bd) bout duration (minutes)
female male stage
16 □ ■ 12 IIa
73 ○ ● 67 II *
63 △ ▲ 62 III

Figure 25: Comparison of the percentage of time male (----) and female (——) oystercatchers spent close (< 6m) to the nest during incubation. Vertical bars represent ± range. Numbers of individuals included in the samples are indicated at the top.


2 3 3 3 5 4 2
100
80
60
40
20
percent time
clutch completion
5 10 15 20 25 30
days after egg-laying
Egg Laying
Incubation
Stage IIa
Stage II
Stage III

not significant when all data for the first half of incubation (Stage II) were combined. One pair was different from the others because the male incubated more than his mate (Pair CB; Appendix 3.2). Reanalysis of these data, excluding this pair, indicated that the sexes were significantly different in the percentage of time spent incubating. During early incubation, males and female engaged in similar numbers of incubation bouts, but those of females were longer and this difference was significant (Fig. 23b, c, 24).

Behaviour of the sexes became more similar as incubation progressed. As in early incubation, males and females spent similar amounts of time close to the nest (Fig. 25). Generally, the difference in the amount of time incubating between males and females decreased until the second half of incubation when the sexes shared incubation duties almost equally (Fig. 23a-c). This reduced difference between the sexes in incubation behaviour occurred in all pairs, regardless of which sex had previously incubated more. Incubation bouts by both sexes increased in duration and became less variable in duration over the incubation period (Fig. 24).

Analysis of the frequency distributions of incubation bout durations again indicated that, overall, females incubated for longer periods than males did (Fig. 24).

This analysis also showed that incubation bouts by both sexes increased in duration and became less variable in length over the incubation period.

There appeared to be no diel pattern in the sharing of incubation duties. Females were incubating at 50 per cent (of 26) of the conclusions of the last watch (approximately 2100 hr). Night observations were conducted three times on different pairs; two pairs were observed during Stage II and one during Stage III. However, it was possible only to record change-overs, showing that both sexes incubated at night, and that bout durations were similar to those during the day.

After considering the differences in the division of effort between incubation stages there was still variation among pairs. As mentioned, one pair differed in that the male incubated more than his mate. Members of another pair (PrB) were different from this and other pairs, in that the female incubated over 80 per cent of the time. The male was inattentive and frequently left the nest before the female returned. This resulted in the only observed predation of an oystercatcher nest, by a gull in this instance.

Since the division of effort was influenced primarily by incubation bout duration, this was used to examine further the differences among individuals. The results of a two-way ANOVA, comparing incubation bout duration for males and females for each of six pairs during Stage II, indicated an overall difference between the sexes ($F_{(1,139)}$=18.1 P<.01) and the same among pairs ($F_{(5,139)}$=3.1 P=.01). A significant interaction between the sexes and pairs suggested that the pattern of variability between sexes differed among pairs ($F_{(5,139)}$=3.2 P=.01). To investigate this, each sex was tested for differences among pairs using a one-way ANOVA followed by a Duncan's Multiple Range Test (Sokal and Rohlf 1981).

Results of the one-way ANOVA suggested that differences existed among the pairs for each sex (females, $F_{(5,72)}$=2.7 P=.02; males, $F_{(5,66)}$=8.7 P<.01), but the results of the multiple range test indicated that there was overlap among the individuals of each sex. Generally, three pairs were similar while the two pairs mentioned above were different from the others and each other, thus accounting for the interaction. This was because the PrB female incubated in very long bouts while her mate exhibited short ones, and the reverse was exhibited by the CB pair. Similar analyses, conducted on incubation bout durations during Stage III, indicated that there were no differences between sexes or among individuals. This supports the previous observation that the behaviour of the sexes became more similar and less variable toward the end of the incubation period.

There appeared to be complimentarity between members of a pair in that one member incubated for long periods and the other for short ones. This in turn influenced the relative participation in incubation by members of a pair; those exhibiting long bouts spent more time incubating. For example, PrB male rarely incubated and the female apparently increased her incubating time to compensate for this. In contrast, the CB female seemed reluctant to incubate. The male of this pair did most of the incubating and incubated for longer bouts than other males did. To examine the factors influencing the duration of incubation bouts, the reasons for departures from the nest were examined.

Duration of incubation bouts did not appear to be influenced by the length of time spent off the nest, either preceding or following the incubation bout, as indicated by the lack of correlation between pre- and post-bouts and incubation bout durations (preceding bout and incubation bout: $r=.12$ n.s. $n=113$; following bout and incubation bout: $r=.13$ n.s. $n=126$). Results were similar whether bouts were compared during early or late incubation stages, or throughout incubation as above. There was no difference between male and female. This suggests that the reason an incubation bout ended may have come from an external stimulus rather than an internal one.

Support for this suggestion comes from from an examination of the context of nest departures. Most of the departures from the nest were due to obvious external factors (approach of conspecific, gull or mate), while 42 per cent (female) and 34 per cent (male) were not (Table 3). Birds departing for reasons other than the approach of conspecific, gull or mate, often returned to the nest to resume incubation rather than changing over. I often noted that when the incubating bird left the nest to pipe with a conspecific or attack a gull (usually the male; see below), the non-incubating oystercatcher usually returned to the nest and commenced incubating. Thus the eggs were almost never left unguarded.

Pair members tended to leave the nest for similar reasons throughout the incubation period (Table 3). However, when data for all incubation stages were considered, males and females differed significantly in how they left the nest (Table 3). Females tended to stand or shuffle eggs more often, while males left to attack gulls or crows more frequently (Table 3).

Most piping exits by females were in response to their piping mates (96% of 80). In contrast, males left the nest to pipe with intruders much more often (51% of 69 (compared with 4% of 80 by females); Chi-square=19.9 d.f.=1 P<.01). Incubating females responded to relatively fewer intrusions

Table 3: Comparisons of departures from the nests by male and female oystercatchers. Significant Chi-square values for intersexual comparisons are indicated (*) (all categories combined). Heterogeneity Chi-square values were non-significant and pairs were pooled within stages.

Stage	Sex	Pipe	Attack gull	Approach of mate	Call to mate	Stand	Walk or BT	Leave
IIa	F	1 (6%)	1 (6%)	2 (12%)	0	1 (6%)	11 (69%)	0
	M	3 (11%)	4 (15%)	4 (15%)	0	1 (4%)	15 (55%)	0
II	F	40 (32%)	1 (1%)	31 (25%)	14 (11%)	18 (14%)	19 (15%)	3 (2%)
	M	30 (30%)	2 (2%)	27 (27%)	7 (7%)	5 (5%)	25 (25%)	3 (3%)
III	F	40 (36%)	2 (2%)	37 (33%)	5 (4%)	11 (10%)	15 (13%)	2 (2%)
	M	39 (45%)	8 (9%)	30 (34%)	4 (5%)	1 (1%)	4 (5%)	1 (1%)
Total	F	81 (32%)	4 (2%)	70 (27%)	19 (7%)	30 (12%)	45 (18%)	5 (2%) *
	M	72 (32%)	14 (6%)	61 (27%)	11 (5%)	7 (3%)	54 (24%)	4 (2%)

Table 4: Comparison of responses to intruding conspecifics by incubating male and female oystercatchers. Significant Chi-square values for intersexual comparisons are indicated (*). Heterogeneity Chi-square values were non-significant and pairs were pooled within stages.

Stage	Incubating sex	Number of intrusions	Number of intrusions responded to by: females	males	
II	females	88	17 (19%)	75 (85%)	*
	males	37	36 (97%)	28 (76%)	
III	females	101	30 (30%)	71 (70%)	*
	males	42	28 (67%)	31 (73%)	

Table 5: Comparison of the percentage of time chicks were brooded during thee twenty-one days after hatching and the percent contribution by female oystercatchers. Each entry is based on data collected during one 4-hour watch.

Time	Age of chick(s) (days after hatching)									
of day	1	3	6	10	12	14	15	16	19	21
0500-0900	98.1	80.3	86.6	38.8	35.4	-	17.5	0	0	1.1
0900-1300	98.9	46.8	11.5	.8	6.1	0	0	0	0	0
1300-1700	98.5	22.2	47.4	0	18.0	15.5	6.2	25.9	0	0
1700-2100	98.4	60.5	90.9	34.4	69.2	23.1	13.1	3.9	0	
0500-2100	98.5	47.3	58.0	16.9	26.9	14.9	7.8	9.4	.4	.2
Percent contribution by female	70.6	63.0	88.7	79.4	83.3	83.1	100	100	100	100
Temperature max.		25	19	29	17.5	20	29	17	29	18
Temperature min.		11	12	13	11	12	12 rain	13	11 rain	14

Table 6: Comparisons of departures from brooding bouts by male and female oystercatchers. Chi-square values for intersexual comparisons are all non-significant. Heterogeneity Chi-square values were non-significant and pairs were pooled within stages.

Stage	Sex	Pipe	Attack gull or crow	Approach of mate	Food	Stand or chick out	Other
IVa	F	8 (40%)	0	5 (25%)	-	7 (35%)	0
	M	11 (42%)	1 (4%)	5 (19%)	-	7 (27%)	2 (2%)
IV	F	8 (13%)	8 (13%)	5 (8%)	25 (42%)	13 (22%)	1 (2%)
	M	10 (29%)	1 (3%)	0	12 (36%)	10 (29%)	1 (3%)
V	F	7 (19%)	1 (3%)	-	14 (39%)	14 (39%)	- -
	M	2 (18%)	3 (27%)	- -	2 (18%)	4 (36%)	- -

by conspecifics than did males, but females responded to a higher percentage when not incubating, which was similar to the response by males (Table 4).

Brood (BRO)

Very young chicks (1 - 2 days old) were brooded almost continuously, and older chicks were brooded intermittently throughout the day until they were about 20 days old (Table 5). As might be expected, brooding appeared to be temperature-dependent and even three-day-old chicks were not brooded continuously during the warm midday (Table 5).

Females did most of the brooding, mainly a result of longer brooding bouts than males (Fig. 26a-c, Table 5). Brooding bouts decreased in duration as the chicks grew older, but females continued to brood for longer bouts than did males (Fig. 27). There were no differences between the sexes in the apparent reason the brooding bout ended, but oystercatchers with older mobile chicks tended to leave them to attack gulls more often than those with newly hatched chicks (Table 6). As with incubating male oystercatchers, brooding males left the chicks to attack conspecifics more frequently than did females (Table 7).

Although females spent more time brooding than males did, there were no differences between the sexes in the

Figure 26: Comparison of (a) percentage of time, (b) frequency, (c) median bout duration of BRO by male (----) and female (———) oystercatchers. Vertical bars represent ± range. Numbers of individuals included in the samples are indicated at the top.

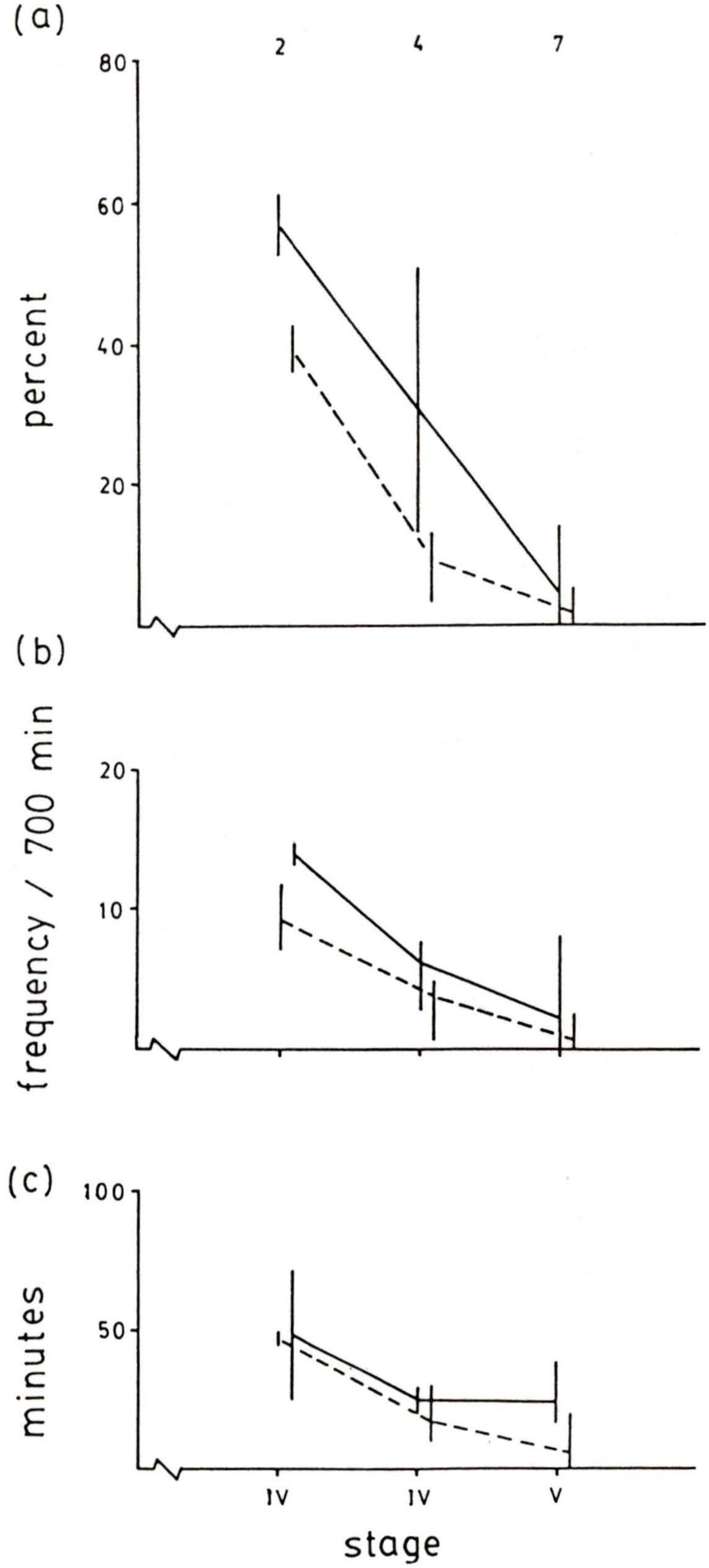
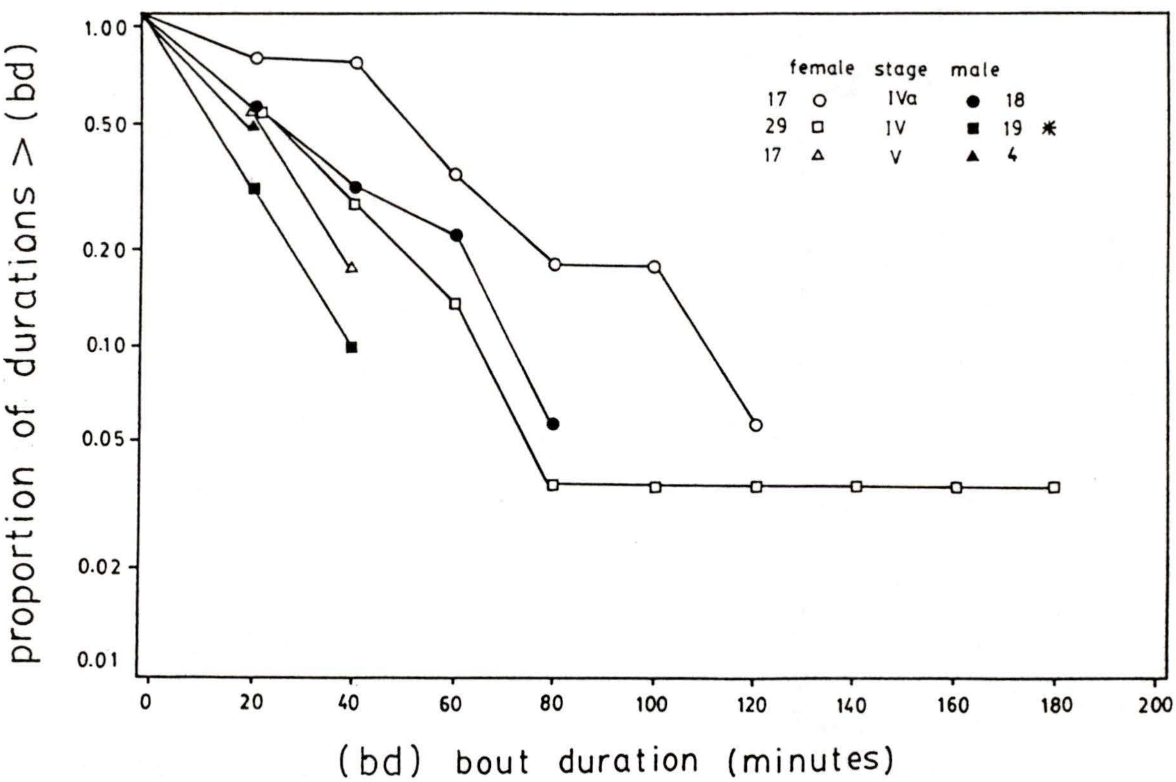
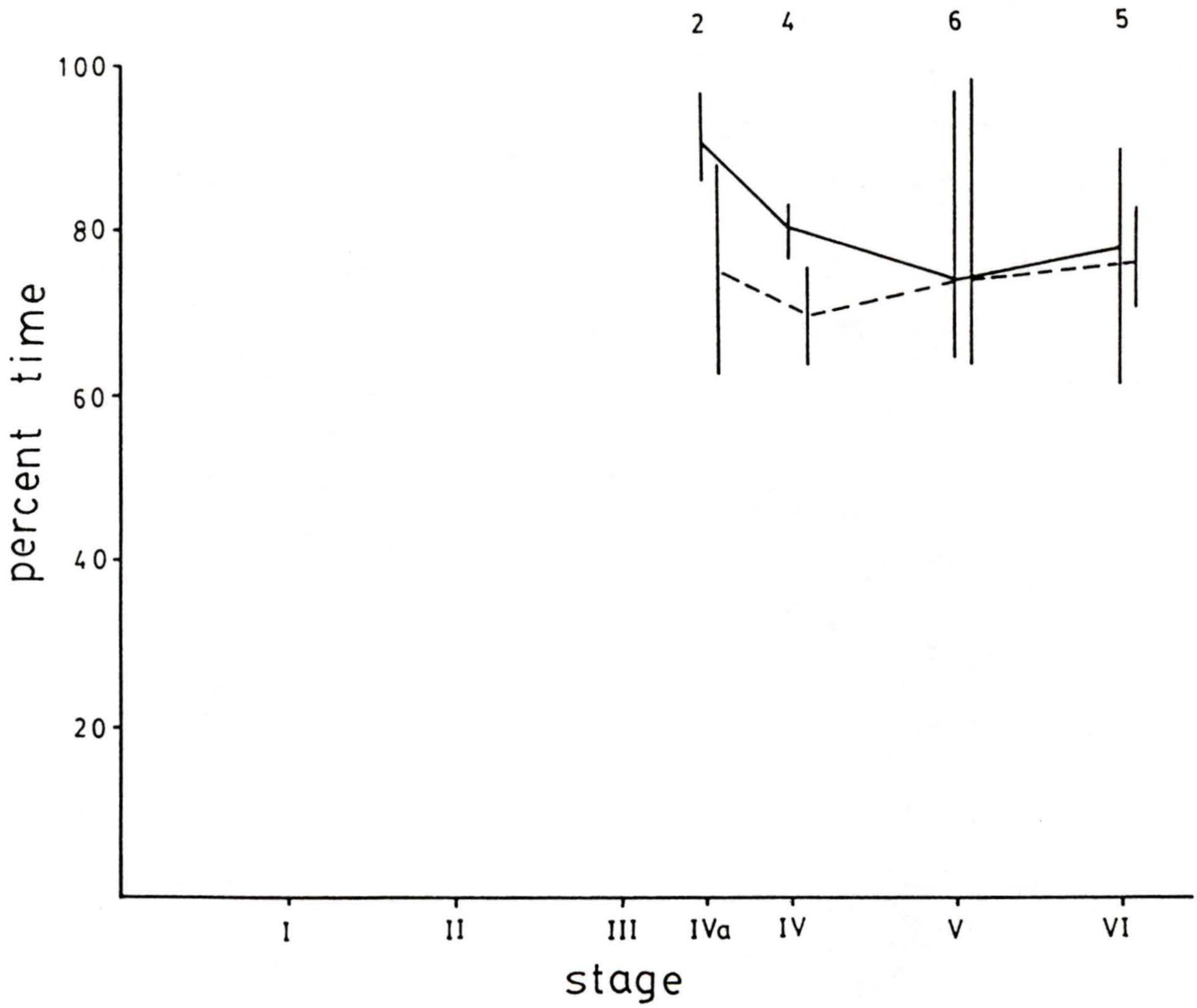

(a)
2
4
7
80
60
40
20
percent
(b)
frequency / 700 min
20
10
(c)
100
50
minutes
IV
IV
V
stage

Figure 27: Comparison of frequency distributions of bout durations of BRO of male and female oystercatchers. None of the Lee-Desu values for intersexual comparisons within stages were significant. Numbers in the symbol legend indicate the number of bouts included in the sample.



proportion of durations > (bd)
1.00
0.50
0.20
0.10
0.05
0.02
0.01
0
20
40
60
80
100
120
140
160
180
200
(bd) bout duration (minutes)
female stage male
17 IVa 18
29 IV 19 *
17 V 4

Figure 28: Comparison of the percentage of time male (----) and female (——) oystercatchers spent close (< 6m) to the chick(s). Vertical bars represent ± range. Numbers of individuals included in the samples are indicated at the top.


2
4
6
5
100
80
60
40
20
percent time
I
II
III
IVa
IV
V
VI
stage

amount of time spent close to the chick and this prevailed after the chicks joined the adults on the foraging ground (Fig. 28).

Feed chick (FC) and forage for chick (FFC)

Males brought a few items to feed to the chicks on the day they hatched. The single item brought by one male was eaten by its chick, while the other male ate all three items he brought.

Most chicks remained at the nest for about ten days after hatching (Stage IV) where the adults brought food to them. Males brought food to the chicks more often than their mates did and thus spent more time FC and FFC (Fig. 29a, b, d, e). Frequency alone is an inadequate measure of the quantity fed to a chick since food items vary in size. Associated with this are different handling times and different values to the chick(s). Males tended to bring larger food items to the chicks than did females but the difference was significant only for one pair (Table 8).

Some food items brought to the nest were not eaten by the chick (17% of 204). Some appeared to be too large to swallow, while sometimes the chick could not be enticed from under the brooding mate. These items were usually eaten by the adults that brought them. There was no

Figure 29: Comparison of percentage of time, frequency and median bout duration of FC and FFC by male (----) and female (——) oystercatchers. Vertical bars represent ± range. None of the paired t-test values of intersexual comparisons were significantly different. Means joined by horizontal lines on the same level above each graph are not significantly different (Duncan's test). Numbers of individuals included in the samples are indicated at the top.

(a) percentage of time FC

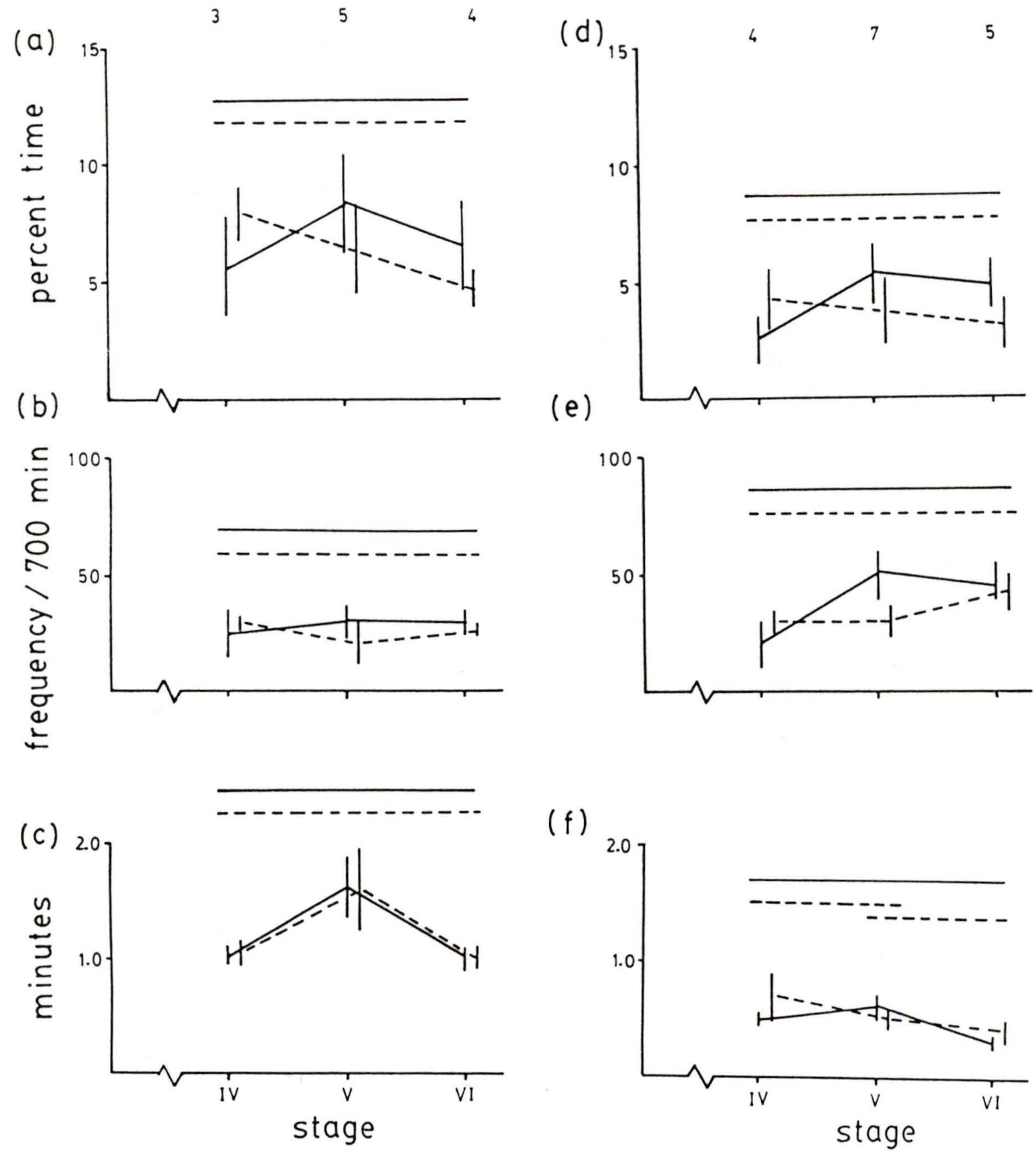
(b) frequency / 700 min FC

(c) median bout duration FC

(d) percentage of time FFC

(e) frequency / 700 min FFC

(f) median bout duration FFC.



(a)
(b)
(c)
(d)
(e)
(f)
3
5
4
4
7
5
percent time
frequency / 700 min
minutes
15
10
5
100
50
2.0
1.0
IV
V
VI
stage

difference between the sexes in the percentage of food item that were rejected or not eaten by the chick (female 17% of 80, male 17% of 124).

Once the chicks joined the adults on the foraging ground and chicks ceased to be brooded (Stage V), females increased the percentage of time they spent FFC and FC to about the level of the males (Fig. 29a-f). This trend was reflected in the frequency with which the birds engaged in FC and FFC, although both sexes also increased the bout durations of FFC (Fig. 29b, c, e, f). Chicks of this age rarely passed up the opportunity to eat, and bouts of FC were shorter than they were during the preceding stages (Fig. 29c).

Generally, the sizes of food items fed to chicks by males and female were similar (Table 9). However, males in some pairs tended to feed their chicks a higher percentage of large items (Table 9).

As the chicks grew older (>30 days; Stage VI) they obtained more food for themselves and the percentage of time adults spent FC and FFC decreased correspondingly (Fig. 29a-f). The sexes were similar in the percentage of time spent FC and FFC mainly because they engaged in these at a similar rate (Fig. 29b, e). Bouts of FFC also decreased in duration (Fig. 29c, f). Oystercatchers with older chicks usually did not initiate feeding bouts.

Table 7: Comparison of responses to intruding conspecifics by brooding male and female oystercatchers. Significant Chi-square values for intersexual comparisons are indicated (*). Heterogeneity Chi-square values were non-significant and pairs were pooled within stages.

Stage	Brooding sex	Number of intrusions	Number of intrusions responded to by: females	males	
IVa	females	22	6 (27%)	14 (63%)	*
	males	22	12 (54%)	8 (36%)	
IV	females	21	5 (24%)	19 (90%)	*
	males	12	7 (58%)	8 (67%)	

Table 8: Size of food items fed to chicks by male and female oystercatchers during Stage IV. Significant values from Fisher Exact tests for intersexual comparisons are indicated (*). Heterogeneity Chi-square value was significant and pairs were not pooled.

Pair	Sex	< size of bill tip	> size of bill tip	
CB	F	10 (83%)	2 (17%)	
	M	13 (87%)	2 (13%)	
JS	F	14 (87%)	2 (13%)	*
	M	17 (43%)	23 (57%)	
AI	F	9 (69%)	4 (31%)	
	M	5 (33%)	10 (67%)	
N41	F	27 (66%)	14 (34%)	
	M	32 (62%)	20 (38%)	

Table 9: Size of food items fed to chick(s) by male and female oystercatchers during Stage V. Significant values from Chi-square (*) or Fisher Exact test (**) for intersexual comparisons are indicated. Heterogeneity Chi-square value was significant and pairs were not pooled.

Pair	Sex	< size of bill tip	> size of bill tip	
GR	F	10 (28%)	26 (72%)	
	M	8 (38%)	13 (62%)	
PB	F	20 (43%)	26 (57%)	
	M	17 (68%)	8 (32%)	
N22	F	50 (86%)	8 (14%)	
	M	76 (76%)	5 (24%)	
AI	F	100 (77%)	30 (23%)	
	M	58 (68%)	27 (32%)	
N55	F	9 (33%)	18 (67%)	
	M	4 (27%)	11 (73%)	
N41	F	20 (54%)	17 (46%)	
	M	9 (28%)	23 (72%)	
JS	F	100 (97%)	3 (3%)	**
	M	65 (87%)	10 (13%)	
JS	F	213 (85%)	38 (15%)	*
	M	113 (69%)	50 (31%)	

Instead, chicks followed closely behind the adults when they were foraging and rushed in to grab the food item. Adults with older chicks were often harassed by the chicks who poked them and nibbled their bills. In an attempt to provide food for these chicks, these adults frequently attempted to forage when the tide was high, and were often washed by waves in their attempts to do so. The chicks did not seem to favour either sex with this attention.

Most chicks began to make foraging trips to nearby islands and reefs with the adults when they were about 60 days old. Both adults accompanied the chicks on most of these off-island foraging trips, but on two occasions the male accompanied the chick, and the female remained on the territory. On another occasion the male returned to the territory 53 minutes before the female and chick returned.

Summary of differences between sexes and among stages

A summary of the time-activity budget of male and female Black Oystercatchers is outlined in Figure 30. To facilitate comparison between the sexes, the cumulative percentages of time each sex spent in major activities over the breeding season are also plotted, one against the other (Fig. 31-34).

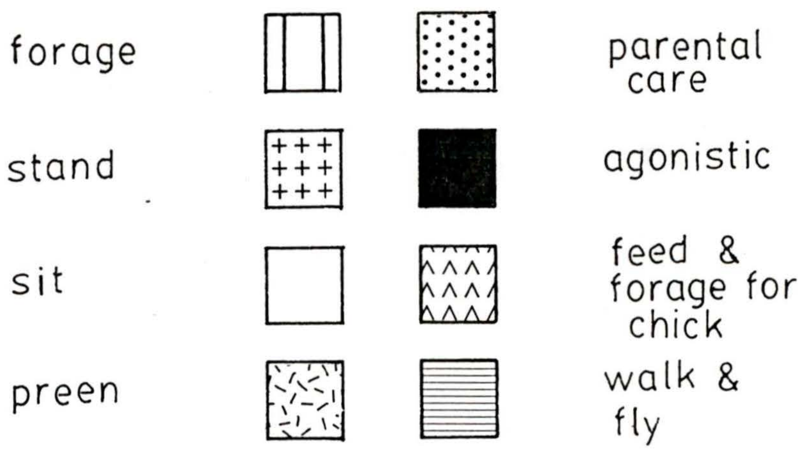
Both sexes spent the most time foraging prior to egg-laying and the least just after hatching (Fig. 30). Generally, females and males spent similar amounts of time foraging, except prior to egg-laying, when females foraged more than did males (Fig. 31). Oystercatchers spent more time foraging off the island before eggs were laid then during subsequent stages, and the least just after hatching. Prior to egg-laying, mates went off the island together, but alone afterward, leaving the mate to stay with the eggs or chicks.

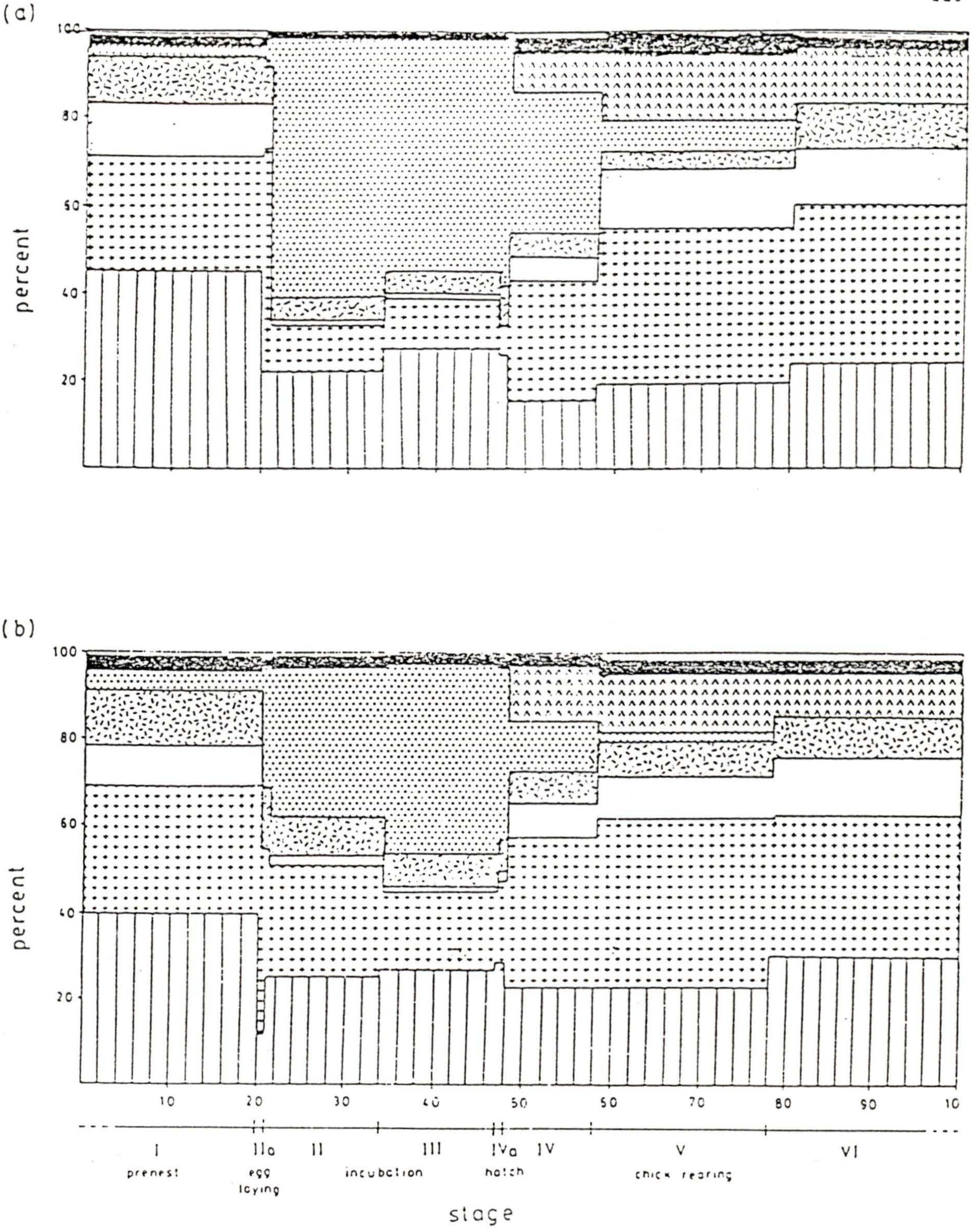
Both sexes spent more time standing after hatching than during previous stages (Fig. 30). Males spent substantially more time standing during all stages than did females (Fig. 32).

The behaviour that showed the most change with the advancement of the breeding season was sitting. Both sexes spent more time sitting before and after incubation than while they had eggs (Fig. 30). In fact, incubating oystercatchers rarely sat. Females and males sat for similar amounts of time until the eggs hatched, after which females spent more time sitting than did their mates (Fig. 32).

Incubating oystercatchers preened less than they did before and after nesting (Fig. 30). During most stages, males spent more time preening than did females (Fig. 31).

Figure 30: Time-activity budget of (a) female and (b) male oystercatchers during the breeding season. Column widths are proportional to the number of days in each stage. The vertical length of each column segment represents the average duration of an activity.





(a)
percent
100
80
60
40
20
(b)
percent
100
80
60
40
20
10
20
30
40
50
50
70
80
90
10
I
IIa
II
III
IVa
IV
V
VI
prenest
egg laying
incubation
hatch
chick rearing
stage

Figure 31: Comparison of the cumulative percentage of time female and male oystercatchers spent FOR and PR behaviours over the breeding season. Note that scales on the axis differ for the two behaviours.

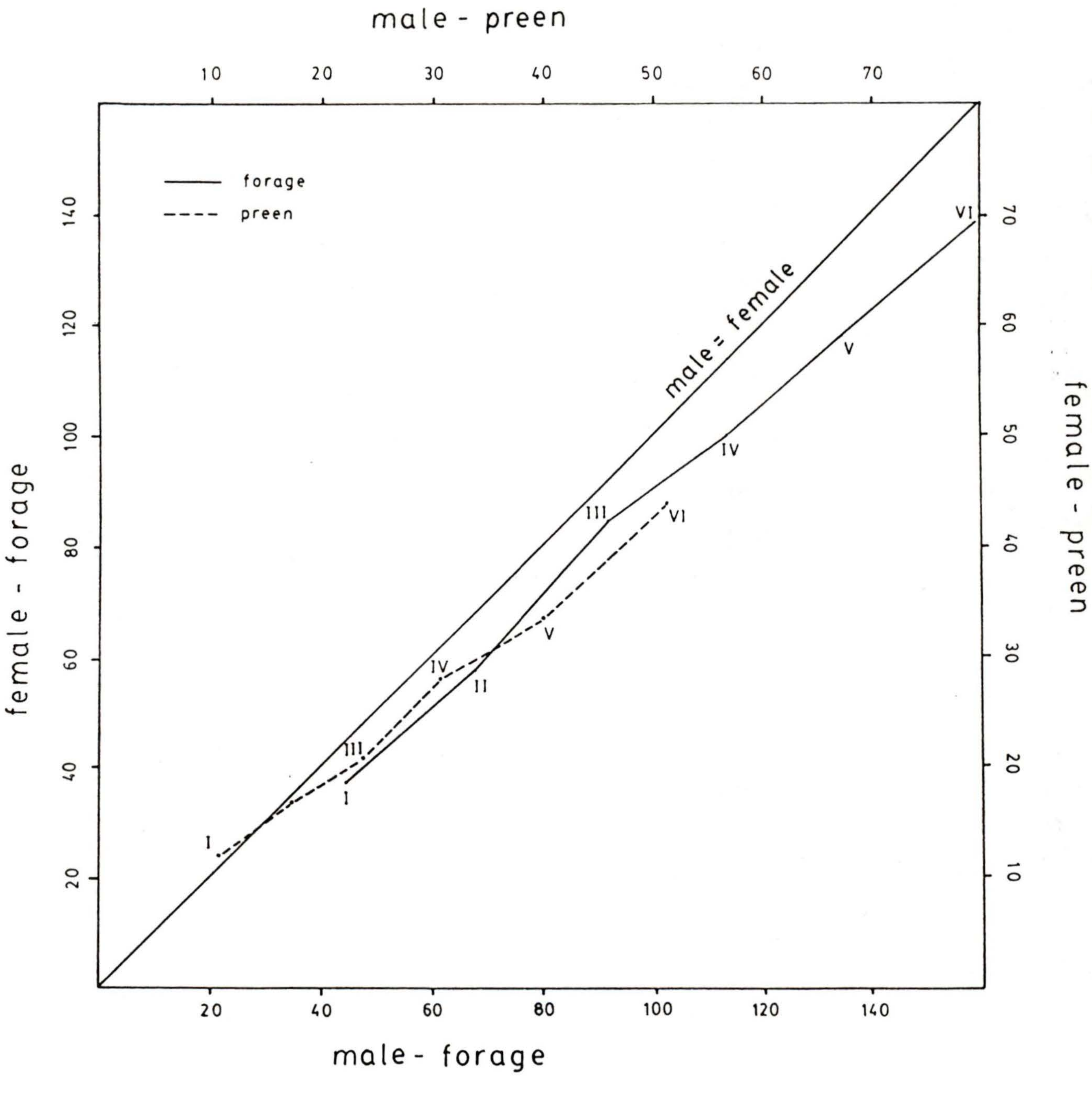
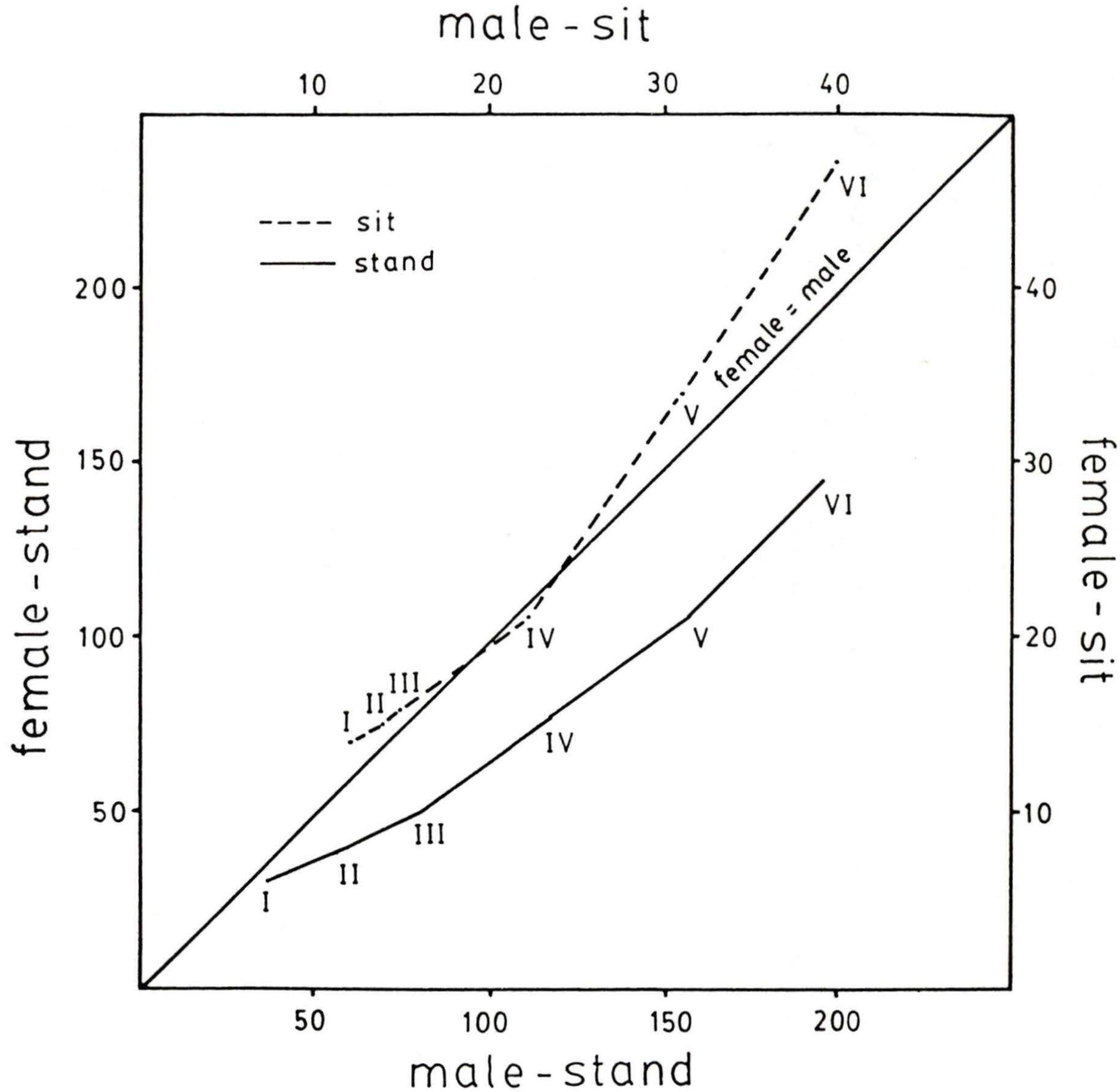

male - preen
10
20
30
40
50
60
70
forage
preen
male = female
female - forage
140
120
100
80
60
40
20
female - preen
70
60
50
40
30
20
10
I
II
III
IV
V
VI
20
40
60
80
100
120
140
male - forage

Figure 32: Comparison of the cumulative percentage of time male and female oystercatchers spent in ST and SI behaviours over the breeding season. Note that the scales on the axis differ for the two behaviours.


male - sit
10
20
30
40
sit
stand
female = male
VI
V
IV
III
II
I
200
150
100
50
40
30
20
10
female - stand
female - sit
50
100
150
200
male - stand

Oystercatchers spent the most time exhibiting agonistic behaviours before and after incubation (Fig. 30). Prior to egg-laying, agonistic behaviours were directed mainly at conspecifics. Throughout the breeding season, males were more aggressive toward conspecifics than were females (Fig. 33). Males maintained relatively high levels of intraspecific aggression until late in the breeding season, whereas females became much less aggressive toward conspecifics after eggs were laid. During incubation, males frequently left the nest to respond to the approach of a conspecific, which is in contrast to females.

After hatching, both sexes sharply increased the amount of time directing agonistic behaviour toward other species. This increase was greater for females, whose cumulative percentage of time spent in this behaviour was greater than males' at the end of the breeding season (Fig. 33).

By the end of the breeding season the cumulative percentage of time females participated in parental care (nest-building, incubating, brooding, feeding and foraging for chicks) exceeded that by males (Fig. 34). However, prior to and during egg-laying, male participation, through nest-building and covering the incomplete clutch, was greater than females' (Fig. 30 and 34). Females increased their participation after the clutch was completed by incubating more than did their mates (Fig. 30). Females

Figure 33: Comparison of the cumulative percentage of time male and female oystercatchers spent in intraspecific and interspecific aggression over the breeding season. Note that the scales on the axis differ for the two behaviours.

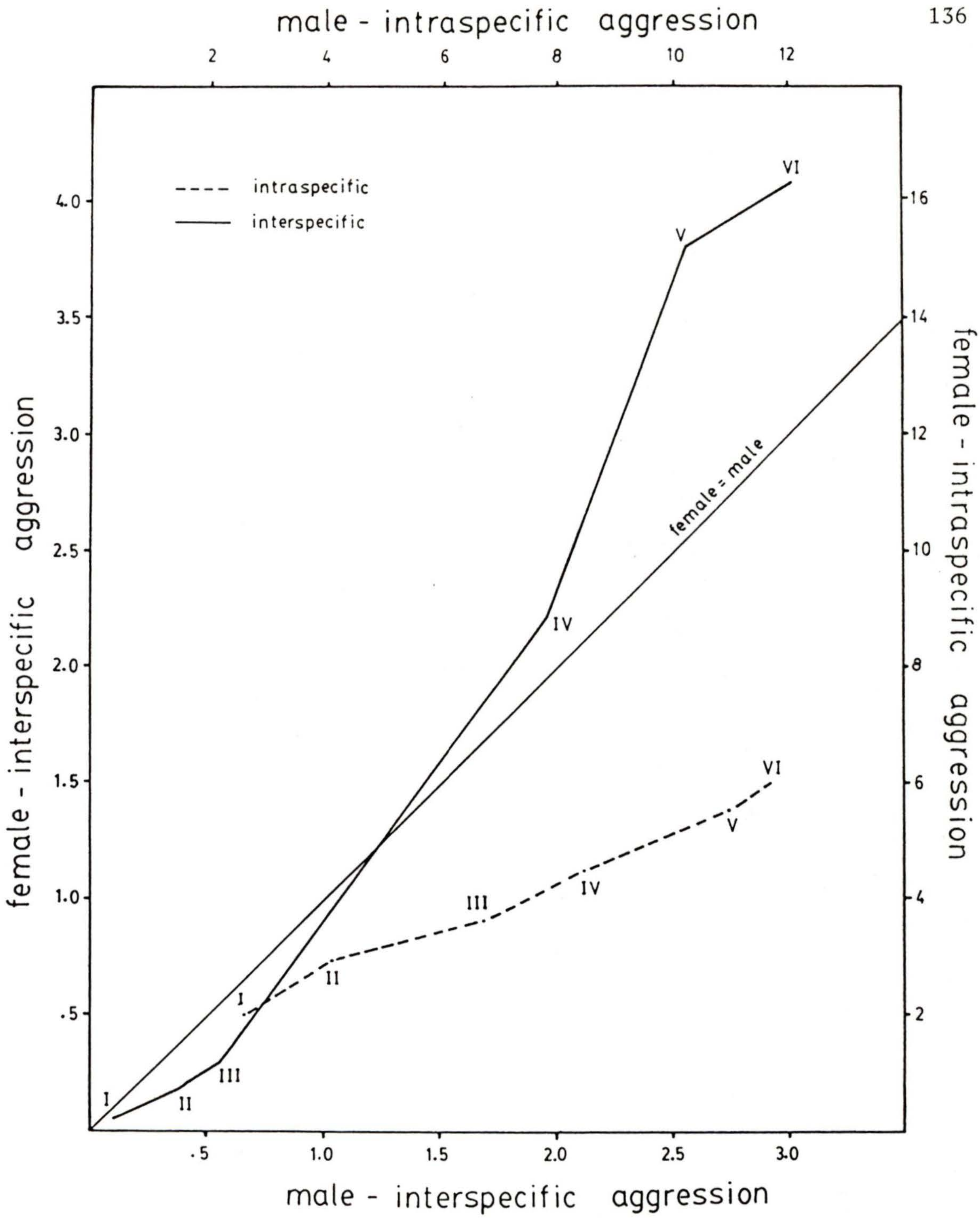
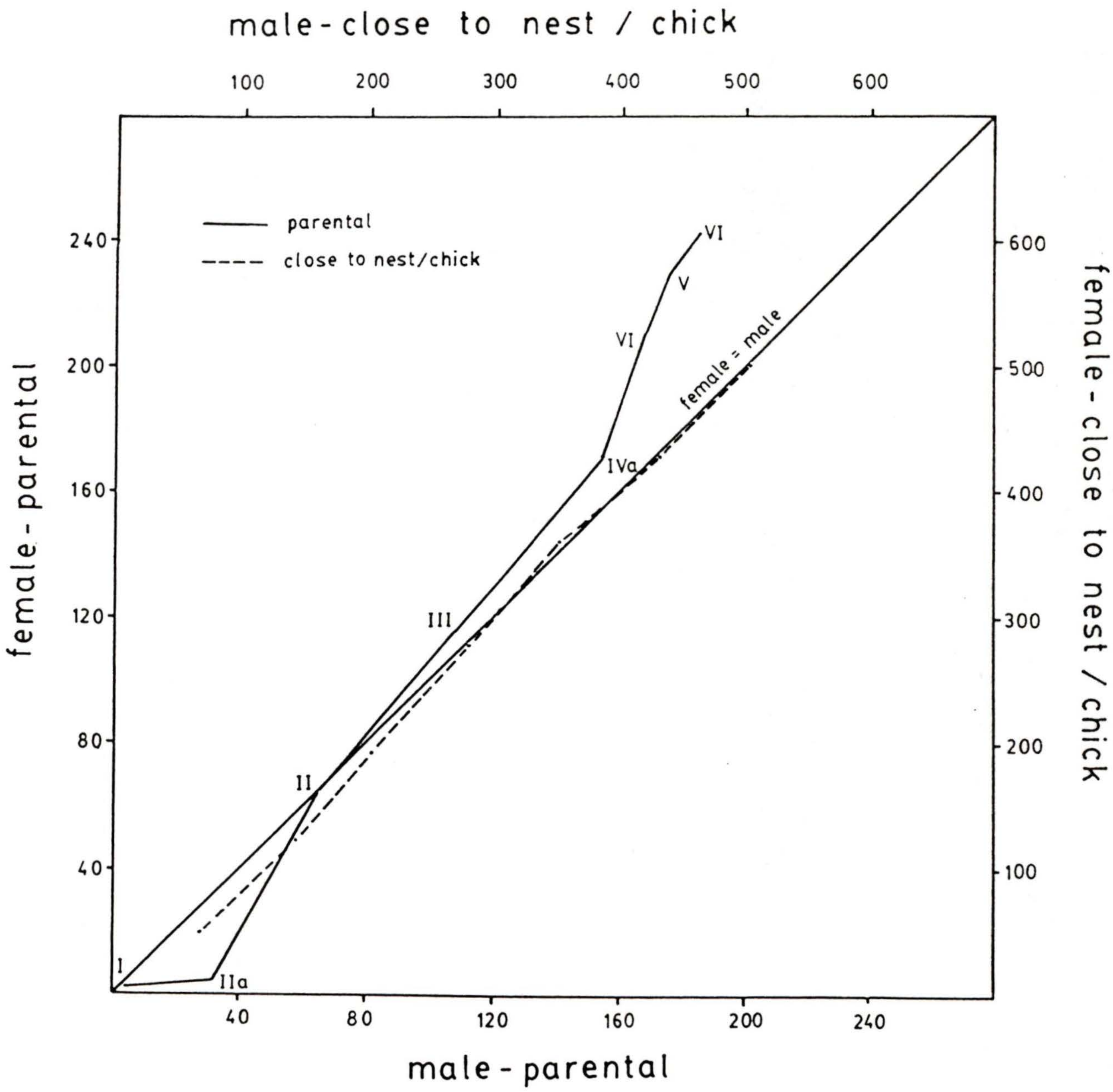

male - intraspecific aggression
2
4
6
8
10
12
intraspecific
interspecific
female = male
female - interspecific aggression
4.0
3.5
3.0
2.5
2.0
1.5
1.0
.5
female - intraspecific aggression
16
14
12
10
8
6
4
2
I
II
III
IV
V
VI
.5
1.0
1.5
2.0
2.5
3.0
male - interspecific aggression

Figure 34: Comparison of the cumulative percentage of time male and female oystercatchers spent in PC behaviours and amount of time spent close to the nest and chicks over the breeding season. Note that the scales on the axis differ for the two behaviours.



male-close to nest / chick
100
200
300
400
500
600
parental
close to nest/chick
240
200
160
120
80
40
600
500
400
300
200
100
VI
V
VI
female = male
IVa
III
II
I
IIa
40
80
120
160
200
240
male-parental
female-parental
female-close to nest / chick

also did most of the brooding. Males tended to feed chicks more just after hatching and males of some pairs fed their chicks larger items than did females. Parents of older chicks participated similarly in feeding and foraging for the chicks (Fig. 30).

Although there were sexual differences in participation in parental care, the sexes were similar in the amount of time they spent close to the nest and chicks (Fig. 34). This measure included the time oystercatchers spent within 6m of the nest and chicks regardless of behaviour.

Finally, oystercatchers generally were more alert after hatching than during previous stages. Oystercatchers with unfledged chicks had shorter foraging, sitting and preening bouts. They also spent more time in alert standing behaviours. Males tended to be more alert than females throughout the breeding season. They spent more time standing and less time sitting than did females. Males also tended to forage in shorter bouts during all stages and their preening bouts were shorter, at least during incubation stages.

Differences among individuals

Several sexual trends were identified in the preceding analyses which were based on data for all pairs combined. What patterns appear when data on individual oystercatchers are analyzed? Generally, multivariate analyses, using MDS, supported trends identified by univariate analyses but with interesting insights that assist in the interpretation of the data.

In the following analyses the arrangement of individuals, in the space defined by the axes (dimensions), was similar whether or not the percentage of time spent foraging was adjusted or whether "off-territory" was included or excluded.

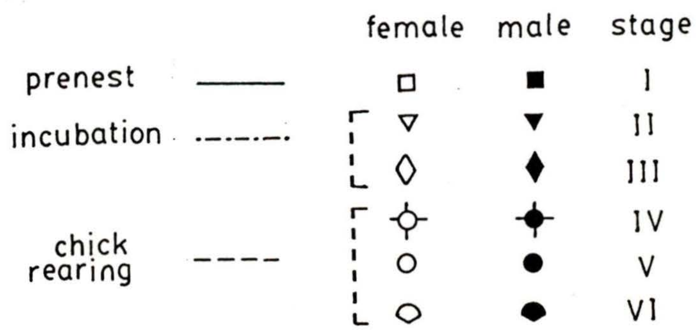
Analysis based on percentage of time reflected univariate analysis in showing the changes in behaviour over the breeding season (only behaviours common to all stages were included in these analyses). That is, most oystercatchers with chicks had higher scores on the first dimension and were dissimilar to oystercatchers with eggs, which had low scores on this dimension, while oystercatchers without eggs or chicks (prenesting) were intermediate (Fig. 35a). Univariate analyses indicated a trend toward decreasing alertness and aggression at the onset of incubation followed by an increase in both after hatching; this appears to be reflected in the arrangement

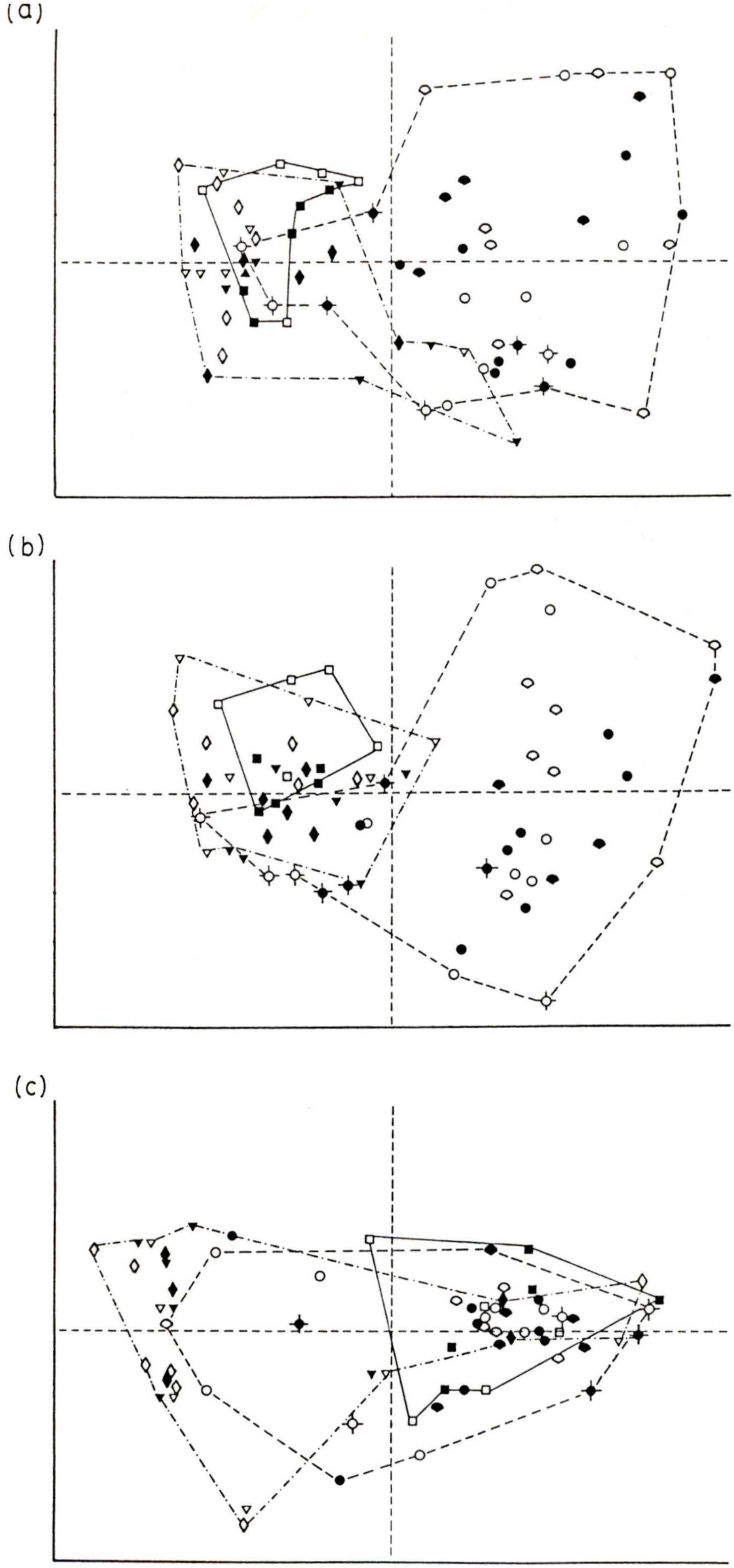
Figure 35: Arrangement of all individuals from all stages of the breeding season in two dimensional space by MDS.

a) percentage of time (stress=.163, RSQ=.878)

b) frequency / 700 min (stress=.179, RSQ=.866)

c) median bout duration (stress=.106, RSQ=.957)




(a)
(b)
(c)

of individuals by MDS described above.

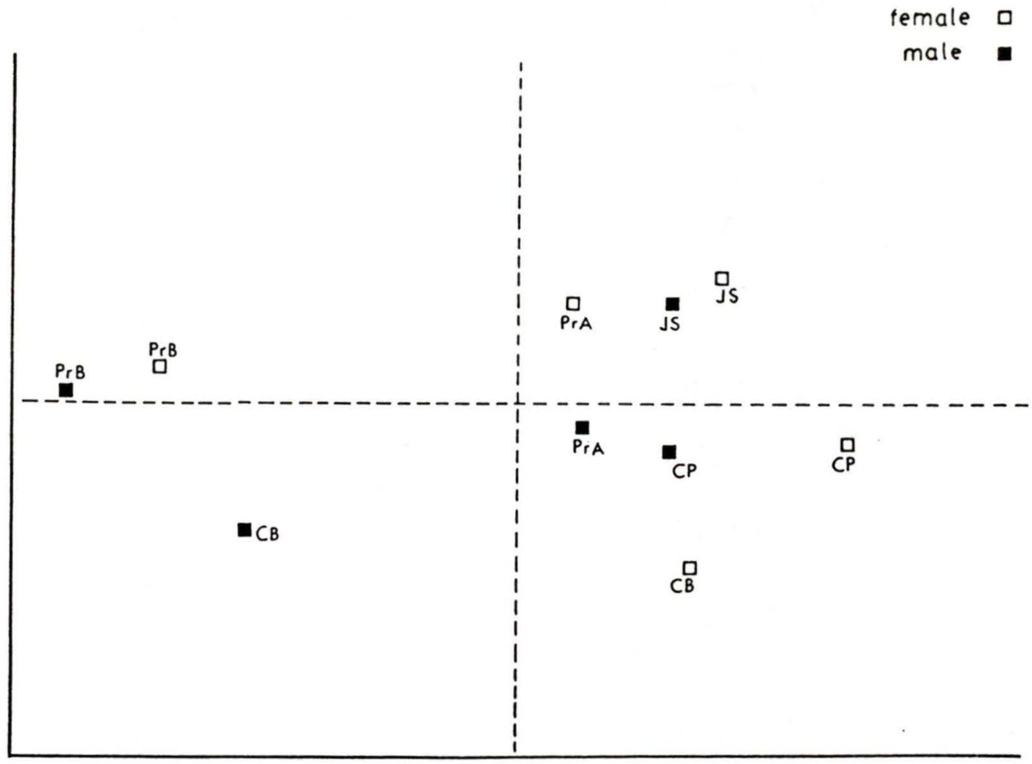
This general arrangement of individuals based on the percentage of time spent in behaviours was similar to MDS of individuals based on the frequency of the behaviours but not on median bout duration (Fig. 35b, c). Univariate analyses also showed that the percentage of time spent in a behaviour was influenced more often by the frequency than by the bout duration of the behaviour.

Although MDS was conducted on the three measures made on the oystercatcher's behaviour, percentage of time, frequency, and median bout duration, results of MDS on frequency and median bout duration data often supported results based on percentage of time or provided no meaningful results. For these reasons, only the results of MDS of percentage of time spent in behaviours are presented in the remainder of this section.

It was difficult to distinguish sexual trends when individuals in all stages were included in the analysis. What patterns appear when data for individuals within stages are analyzed?

MDS of prenesting individuals (Stage I) revealed several striking trends: behavioural similarity but consistent sexual differences within pairs, despite variation among pairs.

Figure 36: Arrangement of individuals in Stage I in two dimensions by MDS on the basis of percentage of time spent in behaviours (stress=.045, RSQ=.990). Individuals are identified using letter codes (refer to Appendix 2).


female
male
PrB
PrB
PrA
JS
JS
PrA
CP
CP
CB
CB

Birds were strongly similar to their mates although there were large differences among pairs (Fig. 36). Even so, there was a clear trend of males having lower scores than their mates on the first dimension (Fig. 36).

These results suggest that pair membership strongly influences behaviour and may obscure differences related to sex. However, the lower scores of males on the first dimension may reflect the results of univariate analysis in showing the male's greater alertness and participation in parental behaviours (nest building).

In contrast to prenesting individuals, MDS of individuals in incubation stages (Stage II and III) revealed behavioural similarity within sexes with explainable exceptions. Analysis of individuals on the basis of the percentage of time showed a trend of males having lower scores on the first dimension (Fig. 37a). This arrangement seemed to be influenced mainly by parental behaviour (cf. below). In this, members of CB pair contrast with other pairs in that the female, which incubated much less than her mate did during Stage II, is similar to males while her mate is grouped with females (Fig. 37a). Members of PrB and N31 pairs were the most dissimilar to each other; the males rarely incubated (during Stage II) leaving their mates to do more than 70 per cent of the incubating.

MDS also supported the trend shown by univariate analysis of decreasing difference between the sexes toward the end of incubation (Stage III). Stage III individuals were more similar to each other than Stage II individuals were (Fig. 37a).

Analysis of individuals, excluding parental behaviour also revealed behavioural similarity between the sexes, but the separation was not as clear (Fig. 37b). Again, males had lower scores on the first dimension suggesting that, in addition to parental behaviour, factors such as alertness and level of aggression distinguished the sexes during these stages.

MDS of individuals with chicks (Stage IV-VI) supported trends shown by univariate analyses, that the behaviour of the sexes became more similar with the advance of the breeding season. Analysis of these individuals failed to show distinct sexual trends with the exception of individuals with young chicks (Fig. 38a). This analysis showed that the Stage IV females were more similar to each other than they were to individuals in other stages, having higher scores on the first dimension and lower scores on the second (Fig. 38a). Stage IV males also tended to have high scores on the first dimension (except N41). Parental behaviour, particularly brooding, seemed to be the main influence on these arrangements since most of the

Figure 37: Arrangement of individuals in Stage II and III in two dimensional space by MDS. Individuals are identified using letter codes (refer to Appendix 2).

a) including parental behaviour (stress=.100, RSQ=.975)

b) excluding parental behaviour (stress=.182, RSQ=.864)

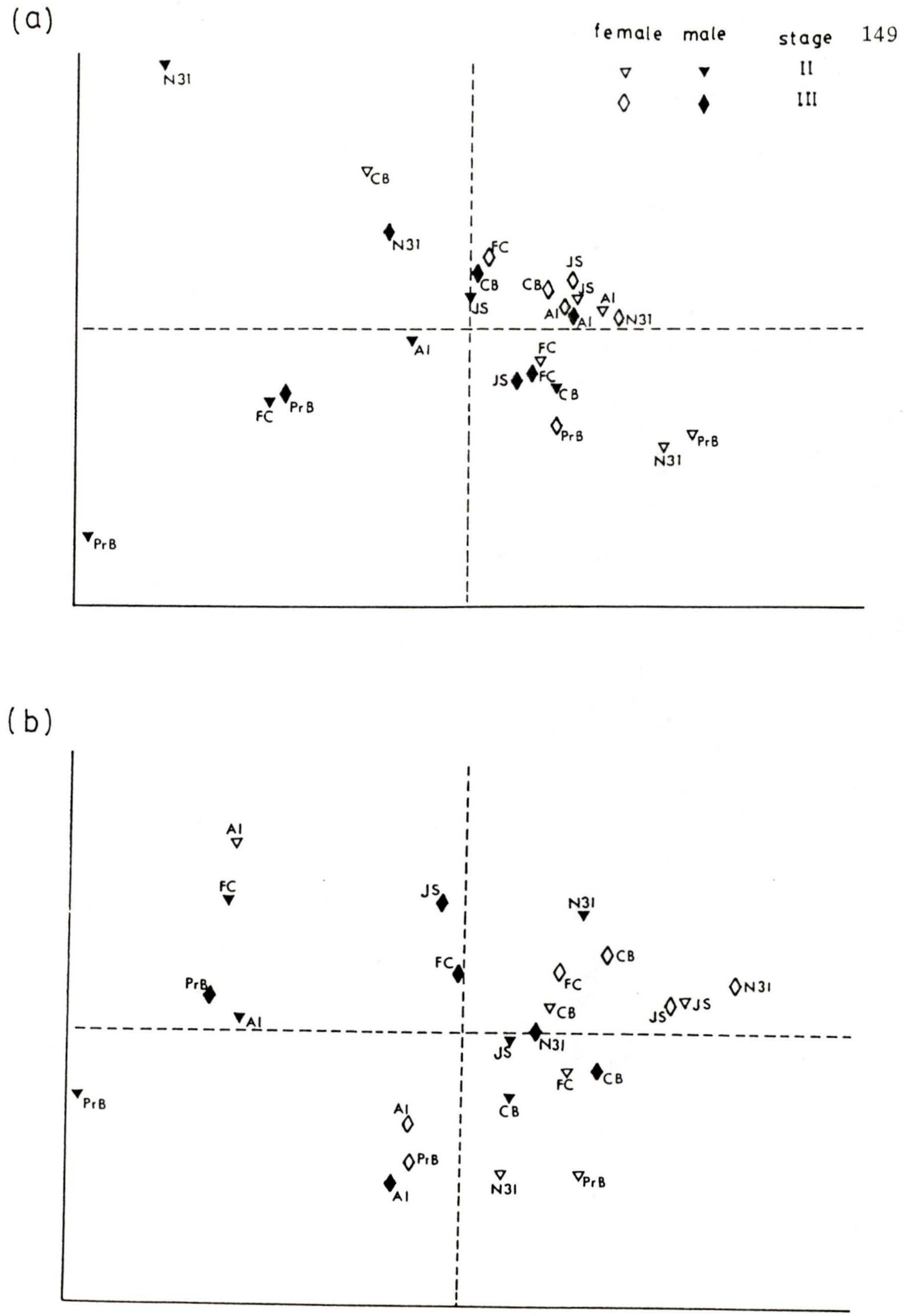

(a)
female male stage
II
III
N31
CB
N31
FC
CB
JS
JS
CB
JS
AI
AI
AI
N31
AI
FC
JS
FC
CB
FC
PrB
PrB
PrB
N31
PrB
(b)
AI
FC
JS
N31
CB
FC
FC
PrB
N31
CB
JS
JS
AI
JS
N31
FC
CB
PrB
AI
CB
PrB
N31
PrB
AI

Figure 38: Arrangement of individuals in Stage IV, V, and VI in two dimensional space by MDS. Individuals are identified using letter codes (refer to Appendix 2).

a) including parental behaviours (stress=.138, RSQ=.926)

b) excluding parental behaviours (stress=.156, RSQ=.886)

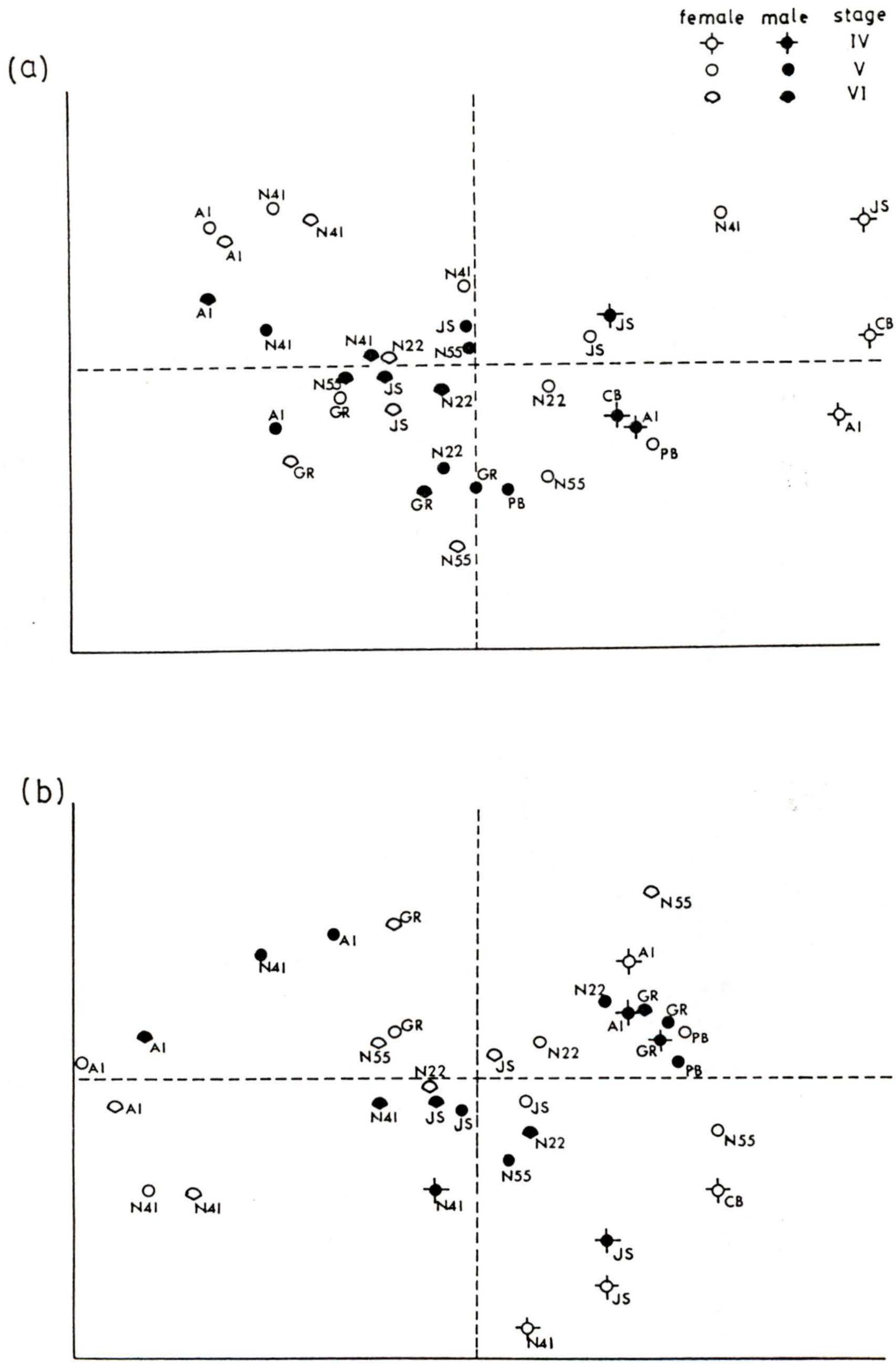
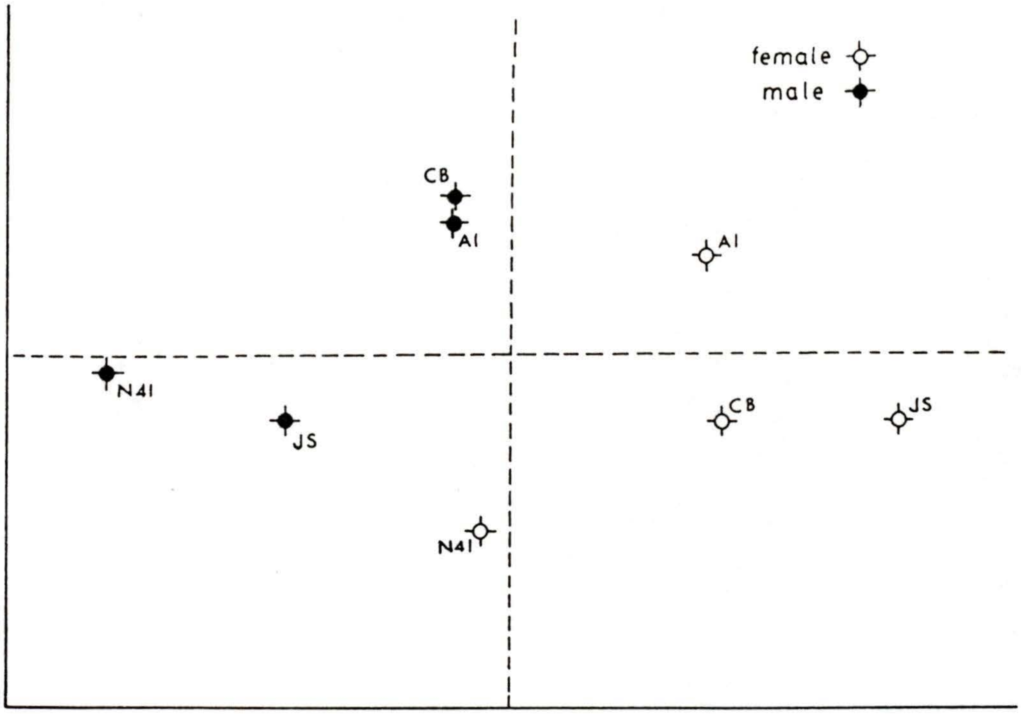

female male stage
IV
V
VI
(a)
(b)
N41
A1
JS
CB
N22
N55
GR
PB

Figure 39: Arrangement of individuals in Stage IV in two dimensional space by MDS. Individuals are identified using letter codes (refer to Appendix 2).

a) including parental behaviour (stress=.025, RSQ=.996)

b) excluding parental behaviour (stress=.050, RSQ=.982)

(a)



(b)

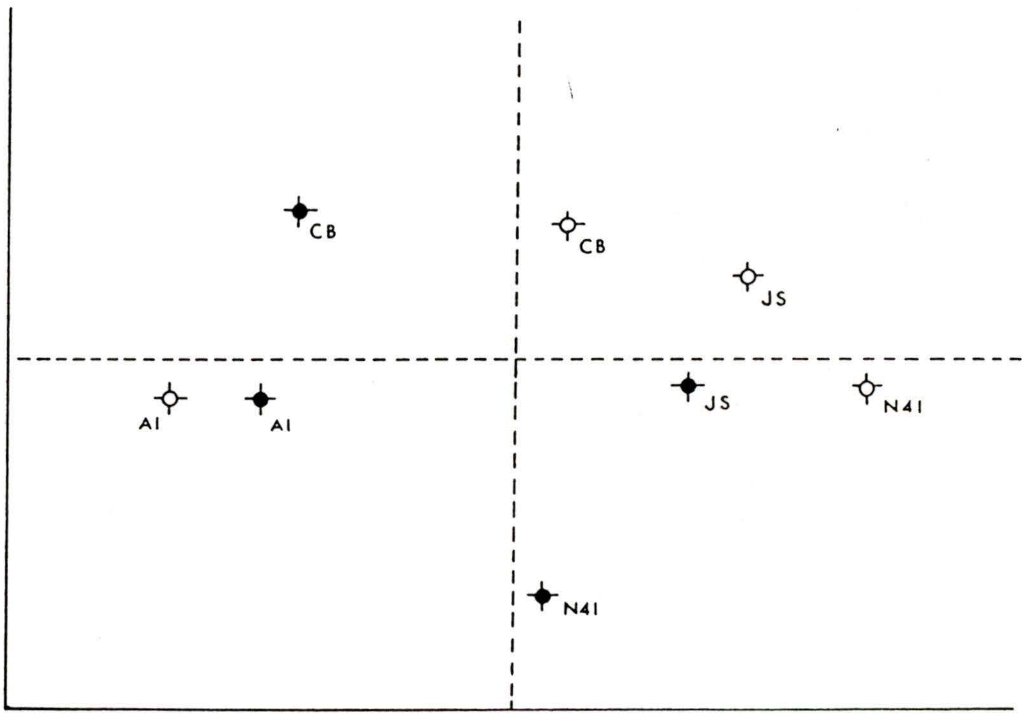
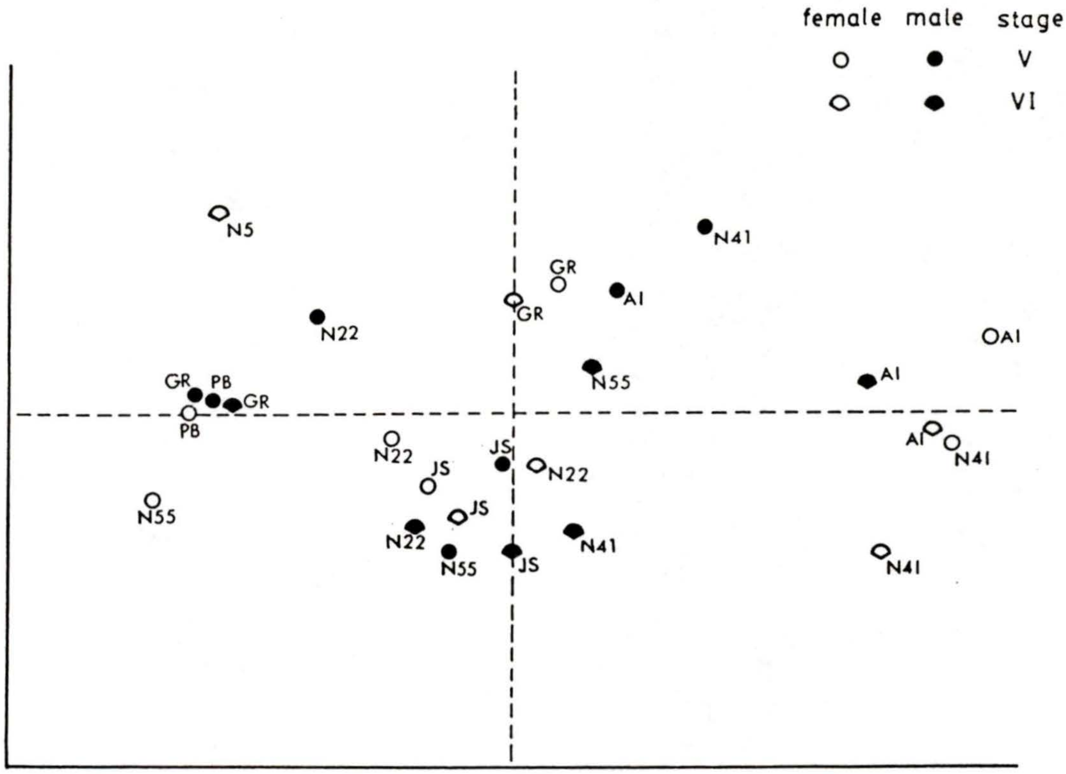


Figure 40: Arrangement of individuals in Stage V and VI in two dimensional space by MDS (stress=.164, RSQ=.882). Individuals are identified using letter codes (refer to Appendix 2).


female male stage
V
VI
N5
N41
GR
A1
GR
N22
OA1
N55
A1
GR PB GR
PB
A1
N41
N22
JS
JS
N22
N55
JS
N22
N41
N55
JS
N41

individuals that brooded in Stage V were similar to Stage IV individuals (Fig. 38a). Further support for this came from analysis that excluded brooding, which produced an arrangement with a trend toward behavioural similarity between pair members instead of similarity among members of the same sex (Fig. 38b).

Analysis of Stage IV individuals alone revealed distinct sexual differences with females having higher scores on the first dimension (Fig. 39a). Again, parental behaviour seemed to be the main influence because when brooding was excluded from analysis, individuals were arranged independently of sex and pair members were similar (Fig. 39b).

The increased similarity among pairs toward the end of the breeding season was emphasized by MDS of individuals in Stage V and VI. This analysis showed that there was strong similarity within pairs, particularly for those pairs with fledged chicks (Stage VI) (Fig. 40). This arrangement of individuals was similar whether parental behaviours were included or not.

V DISCUSSION

The sampling procedure is an important feature of this study. Some researchers studying shorebird behaviour take the approach of studying one pair in detail and assume that their behaviour is typical of the species (e.g. Ashkenazie and Safriel 1979b). Others use units of time rather than individuals as the sampling unit (e.g. Maxson and Oring 1980, Mundahl 1982). Neither approach provides estimates of variability within the population, which is necessary to determine how "typical" a trait is. Examination of variability in relation to specific environmental conditions can provide clues to flexibility or adaptive nature of a trait (Walters 1984, Fitzpatrick 1985, Miller 1985). Numerous descriptive studies exist that identify trends, but in light of the many theories in the literature, it is becoming more obvious that information is necessary at the level of the individual. This method is more time consuming and possible only when individuals are recognizable, a situation that existed in this study.

Results of this study revealed much between-pair variability. This was emphasized by the results of MDS analyses which showed that mates were often more similar to each other than to other birds of the same sex. Although differences in behaviour may be attributed to factors such as age and experience, the consistent trend of similarity between pair members suggests that these differences reflect differences in the qualities of the oystercatchers' territories. The territories on Cleland Island were different sizes and shapes, which influenced the percentage and length of exposure of foraging space. In addition, differences in topography of the territories create differences in the ease with which oystercatchers can monitor their surrounding environment (Metcalfe 1984b). Support for the suggestion that such asymmetries exist among oystercatcher territories on Cleland Island is the observation that not all pairs participated in extra-territorial foraging. Those pairs that did, had territories on the east side of the island, which was the side closest to reefs and other islands. Some of these pairs appeared to have smaller territories than pairs on other parts of the island. Hartwick (1978) suggested that off-island foraging was related to the lack of available prey (particularly mussels) during tides of small amplitude, high surf or slack water.

These asymmetries in territory quality create differences in the amount of time devoted to foraging, vigilance, parental care, etc. Nol (1984) found that differences in biomass between habitats created vast differences in the amount of time two species of oystercatchers spent foraging. Another report of within-species variability has been attributed to differences in habitat quality (Heppleston 1972).

In this study, the influence of differences in territory quality is reduced in the examination of intersexual differences by using comparisons between pair members. However, it cannot be similarly reduced in the comparison among stages. Despite this variability, identifiable trends exist. These trends are emphasized in the comparisons made among stages and among individuals in the multivariate analyses.

Comparable quantitative data on oystercatcher behaviour are available for another population of Black Oystercatchers (Helbing 1977), Blackish (*H. ater*) and American Oystercatchers (*H. palliatus*) (Nol 1984). There are also numerous qualitative descriptions of oystercatchers from which information about parental behaviour can be derived. Comparable quantitative data are available for members of the closely related Recurvirostridae, and the more distantly related Scolopacidae, Charadriidae and Laridae. In this section I will compare the behaviour of the Black Oystercatcher with species in these related groups.

Forage (FOR)

There was no evidence of a diel foraging cycle, which was not surprising since foraging opportunities were controlled by the tidal cycle. Diel foraging patterns have been recorded for the American Oystercatcher in a location where foraging space was always available (Nol 1984).

Only during the prenesting stage was there a sexual difference in the time spent foraging; female Black Oystercatchers spent more time foraging than males did. This has also been reported for Black Oystercatchers in California (Helbing (1977), American and Blackish Oystercatchers (Nol 1984) and for other shorebird species (Gibson 1978, Maxson and Oring 1980). The common explanation for this is that females are building up reserves for egg production. Egg production has been shown to increase energy needs in Willow Ptarmigan (*Lagopus lagopus*) (West 1968) and in Zebra Finches (*Taeniopygia castanotis*) (El-Wailly 1966) and has been suggested for American Avocets (*Recurvirostra americana*) (Gibson 1978) and for oystercatchers (*H. ostralegus finschi*, Baker 1975).

Both females and males spent more time foraging during the prenesting stage (Stage I) than during subsequent stages. It is unlikely that these changes were influenced by changes in prey abundance or ambient temperature, as suggested by Gibson (1978) for avocets, since the mussel beds on Cleland Island were probably stable over the breeding season and temperatures did not fluctuate widely.

In part, the elevated prenesting feeding levels may have been due to the high energetic demands of intraspecific interaction and a subsequent decrease, in incubation stages, due to reduced activity levels. Indirect evidence that the activity levels, mainly territorial defence, prior to egg laying are energetically expensive, is the observed weight loss in the European Oystercatcher (*H. ostralegus*) during the prenesting stage (Mercer 1968, Dare 1977). The incubation phase was found to be a period of reduced energy expenditure in Abert's Towhee (*Pipilo aberti*, Finch 1984), Red-winged Blackbirds (*Agelaius phoeniceus*) and Willow Flycatchers (*Empidonax traillі*) (Walsberg and King 1978).

Incubating and nest guarding probably also limit the amount of time available for foraging. Support for this suggestion comes from the observation that female Spotted Sandpipers (*Actitus macularia*) forage more than males do during all stages (Maxson and Oring 1980). This species usually breeds polyandrously and thus the female is not constrained by incubation duties. Further support comes from the observation that incubating European Oystercatchers show a steady decrease in weight over the first half of incubation (Mercer 1968). That incubation can severely constrain time budgets has been suggested for Black Oystercatchers in another study (Helbing 1977) and other bird species (Norton 1972, Walsberg and King 1978).

Correspondingly, the increase in foraging levels after hatching may reflect both the increased activity levels due to chick defence and the release from the time consuming duty of incubation which kept the birds close to the nest. Helbing (1977) reported a similar pattern in the amount of time Black Oystercatchers in California spent foraging over the breeding season. That foraging levels did not increase to prenesting levels may reflect the continued constraint imposed by chick rearing. Mercer (1968) also suggested that chick-rearing duties reduced the amount of time available for foraging. Further support for this suggestion comes from the report that after incubation, avocets, which do not feed their chicks, surpassed prenesting foraging levels (Gibson 1978).

Nol (1984) suggested that, after hatching, oystercatchers nesting in intertidal habitats were prevented from increasing foraging levels beyond prenesting ones by limits imposed by the fluctuating opportunities for intertidal feeding. This suggestion was based on the observed differences between Blackish Oystercatchers, inhabiting rocky intertidal areas, and the American Oystercatcher, inhabiting areas where food was always available; the latter showed a large increase in foraging after hatching that surpassed prenesting levels, while the former did not. Nol suggested that this limit on foraging negatively influenced reproductive success and indirectly clutch size. Black and Blackish Oystercatchers are similar in that they inhabit rocky intertidal areas and spend similar amounts of time foraging prior to egg-laying (Nol 1984). However, they differed in that Black Oystercatchers did not forage continually when foraging space was available (pers. obs., Hartwick 1978), even when they had chicks, unlike reports for Blackish Oystercatchers (Nol 1984). If increased foraging after hatching leads to an increase in reproductive success, one would expect to see foraging levels to reach prenesting ones, at least. However, after hatching, Black Oystercatchers continued to forage at levels that were below prenesting ones. It is not clear whether Nol included the time spent foraging for the chick in this estimate. However, for the Black Oystercatcher, even if FFC is combined with FOR, the resulting estimate is still less than the estimate for foraging levels prior to egg-laying. As Nol (1984) concludes, foraging after hatching does not appear to be the sole factor influencing reproductive success. On Cleland Island, breeding success appeared to be limited more by the ability of the adult Black Oystercatcher to provision the chicks rather than the availability of food (pers. obs., Groves 1984). Breeding success has been reported to be similarly limited for the European Oystercatcher (Heppleston 1972).

It may be inferred that eggs were not as valuable (Trivers 1972) or perhaps less vulnerable or more easily protected than chicks, since oystercatchers continued to leave the island to forage during incubation but not after hatching.

Relative duration of foraging bouts was an indication of alertness. Males, foraging for shorter bouts, were thus considered to be more alert than females before egg-laying and both sexes were more alert during chick rearing than in previous stages. Foraging bouts during chick rearing are probably shortened by the demands of feeding and foraging for the chick, which could have similar consequences.

Stand and Sit (ST and SI)

Oystercatchers spent the most time standing and sitting when they had chicks and the least when they had eggs. However, the low percentage of time spent in these behaviours during incubation stages is deceptive, since incubating oystercatchers are essentially sitting. It has been shown for most birds, incubation does not increase metabolism over resting levels (review by Grant 1984). Those birds that incubated more sat less, such as females during incubation (Stage II), while neither sex sat much during late incubation (Stage III), when they were participating in incubation almost equally. It could be that the required "rest" was obtained when the bird was incubating. Alternatively, during incubation there could be an increased need to be alert with a greater proportion of overall "resting" being composed of standing.

The greater amount of time spent in the more alert standing behaviours after hatching is probably due to the greater likelihood of predation of mobile young compared to stationary chicks or, alternatively, an increase in the value of the offspring (Trivers 1972). Similarly, American Oystercatchers spend an increased amount of time standing (Nol 1984).

Males spent substantially more time in alert standing behaviours throughout the breeding season than did females. During the prenesting and egg-laying stages, this was probably due to the anticipated intrusions by males and to female vulnerability to potential predators; females spent a large percentage of this time foraging. Ashkenazie and Safriel 1979b found similar sexual differences in this behaviour in Semipalmated Sandpipers (*Calidris pusilla*) and attributed this to similar influences. Following hatching, oystercatchers were alert for the approach of gulls. At this time, males were guarding their mates, which were brooding much of the time, as well as the broods. This is in contrast to Semipalmated Sandpipers in which the female spends the greater amount of time standing after hatching (Ashkenazie and Safriel 1979b). However, in this species the males do most of the brooding.

Both Helbing (1977) and Nol (1984) classified oystercatchers as "standing" only when they had their bills exposed, considering standing and sitting with bill on back as "resting", thus making it difficult to compare among studies. However, it appears that oystercatchers in those studies showed a similar pattern of standing and sitting as Black Oystercatchers did in this study.

Oystercatchers had the longest bouts of SIBOB during prenesting and the shortest during early chick rearing with late chick rearing stages at intermediate levels. I consider the brevity of these bouts to be an indication of alertness. While short bouts during early chick rearing probably indicate an increase in need to be alert, those during late chick-rearing are the result of chicks harassing the adults, and adults responding by standing. Similarly, bouts of STBOB are longest during prenesting and shortest during chick-rearing for similar reasons.

Preen (PR)

Oystercatchers frequently preened after foraging, piping and copulation, and always after returning from foraging trips off the island. Since the incidence of all of these behaviours was highest during the prenesting stage (Stage I), the frequency of occurrence and percentage of time spent preening was also correspondingly higher. The drop in the frequency and amount of time spent preening at the onset of incubation corresponds to the decrease in the occurrence of these activities, but may also reflect the constraining influence of incubation. Oystercatchers sometimes preened while incubating (classed as incubation) and thus the estimates for preening here may be underestimates.

The gradual increase in the amount of time and frequency of preening following hatching may reflect increases in activities that precede preening, but may also reflect a release from constant attention to the eggs and young chicks. Another contributing factor may have been the onset of the postnuptial molt, which would increase the need to preen above the normal requirements for feather care.

I consider shorter preening bouts after hatching to be an increase in the level of alertness, related to the presence of mobile chicks that require more attention than stationary eggs. Similarly, during incubation stages, males tended to be more alert than their mates.

Males preened slightly more than females consistently over the breeding season, perhaps as a result of the greater activity levels of males, particularly in agonistic behaviours. However, the general pattern of increase and decrease over the breeding season closely resembles that of foraging, which probably influenced the amount of preening more than any other activity. Male Semipalmated Sandpipers also tend to preen more than females, which Ashkenazie and Safriel (1979b) also attribute to greater activity by this sex. Helbing (1977) reported that male Black Oystercatchers in California also preened consistently more than females did over the breeding season

The percentage of time American Oystercatchers spent preening before egg-laying (Nol 1984) was similar to Black Oystercatchers in this study. Males of American Oystercatchers also spent more time preening than females did over most of the breeding season. However, in contrast to Black Oystercatchers, American Oystercatchers did not markedly reduce the amount of time they spent preening during incubation, but did during chick rearing. Nol's (1984) estimates, that Blackish Oystercatchers spent less than 3 per cent of the prenesting time preening, seem to be too low to be realistic. Gibson's (1978) findings for avocets are similar in magnitude to mine for Black Oystercatchers, but the avocets preened for the same amount of time throughout all the breeding stages, with a large increase during the postfledging stage, which Gibson attributed to the onset of the postnuptial molt.

Beyond consistencies in sexual differences, there does not appear to be any consistent pattern in the amount of time spent preening over the breeding season among species. I cannot attribute these differences to any particular reason, unless it is differences in sampling technique.

Agonistic (AG)

Although agonistic activities comprised little of the time budget during any stage of the breeding season, they were nevertheless important for defence of the mate, territory and offspring.

Intraspecific interactions (PIPE)

The elevated levels exhibited before egg-laying suggest that some intraspecific aggression served as an anti-cuckoldry mechanism. The slight drop in hostility toward conspecifics after the eggs were laid, but not in the number of intrusions, supports this idea.

Cuckoldry is usually considered to be a threat to males. Males that provide parental care for their mate's offspring must avoid being cuckolded, or they waste time and energy raising someone else's offspring (Wilson 1975, Emlen and Oring 1977, Barash 1982). However, in situations that demand large amounts of male parental care, females can be expected to defend their mates from potential competitors (Orians 1969). This appears to be the situation for the Black Oystercatcher. Females also spent more time interacting with conspecifics before egg-laying than afterward. With mates theoretically guarding each other, a close continuous association between members of a pair would be expected. Black Oystercatcher mates on Cleland Island were rarely apart during the prenesting stage (Stage I), and members of those pairs that foraged off the island usually left and returned together. The protracted prenesting period, with seemingly ineffective copulations exhibited by the oystercatchers in this study and other oystercatcher species (Dircksen 1932, Makkink 1942), may also be interpreted as a mechanism for cuckoldry prevention (Barash 1982).

Although both sexes are susceptible to cuckoldry, males appear to be more threatened by it than are females. Males were more aggressive during the prenesting stage. Most of the attacks on conspecifics by males occurred prior to egg-laying when the threat of cuckoldry was greatest. Males were also more alert, perhaps on the lookout for approaching conspecifics. There are numerous reports of males defending females from other males (Black Rosy Finch (*Leucosticte tephrocotis*), French 1959; Ring Dove (*Streptopelia risoria*), Erickson and Zenone 1976; Mountain Bluebird (*Sialia currucoides*), Power 1980; Black Skimmer (*Rynchops niger*), Burger 1981; Black-billed Magpie (*Pica pica*), Birkhead 1982). That mates of vasectomized male Red-winged Blackbirds have a high rate of fertilized eggs indicates that the threat of cuckoldry is real (Bray *et al.* 1975). Possible cuckoldry has been observed for American Oystercatcher (A. J. Baker, cited by Nol 1984) and I observed a copulation between a male Black Oystercatcher that was a member of a pair, and a female I could not identify.

Males of the European and Variable Oystercatchers (*H. unicolor*) are reported to be more aggressive toward conspecifics on the basis of qualitative information (Huxley and Montague 1925, Buxton 1932, Makkink 1942, Lind 1965, Jones 1979), and Nol (1984) found a similar trend in a quantitative comparison of the sexes of Blackish Oystercatcher, as did Helbing (1977) for Black Oystercatchers in California. However, Nol (1984) found no quantitative difference in the aggressiveness of the sexes of American Oystercatcher prior to egg-laying. It is possible that the latter species was breeding where few non-breeding conspecifics posed a threat of cuckoldry or competition. Support for this comes from the much lower percentages of time spent piping compared with the Black Oystercatcher (American Oystercatcher, female 1.0%, male .7%; Black Oystercatcher, female 2.0%, male 2.8%) and from the lack of replacement of experimentally removed mates. Such replacement occurred rapidly in a similar experiment in the presence of a large non-breeding population of European Oystercatcher (Harris 1970).

Males are also predicted to be the more aggressive sex on the basis of their difference in initial investment in gametes. Females tend to be the more discriminating sex in choosing a mate since they usually invest more per offspring, thus creating competition among males (Wilson 1975, Barash 1982). Other studies of monogamous shorebirds indicate that, although both sexes are aggressive prior to egg-laying, males are more aggressive than females (Gibson 1978, Ashkenazie and Safriel 1979b, Howe 1982, Mundahl 1982). Similar sexual differences have been reported for many gull species (Burger and Beer 1975, Burger 1981, Pierotti 1981, Southern 1981, Butler and Janes-Butler 1984).

Incubating oystercatchers were less aggressive toward conspecifics than prenesting ones, even though conspecifics continued to intrude at approximately the same rate. That territory holders continued their hostility toward conspecifics once the threat of cuckoldry was past (but see below) may be taken as an indication that this aggression was also in defence of the territory, as suggested for the European Oystercatcher (Lind 1965, Harris 1970). This aggression probably also defends the eggs and chicks, since foreign oystercatchers were shown to be a threat to chicks in this study and others (Webster 1941, Hartwick 1974). Support for this comes from the observation that conspecifics landing on a territory were almost always chased, while territory holders reduced the number of times they joined piping parties in comparison with prenesting levels.

During the incubation stages, males continued to respond to almost all foreign oystercatchers on the territory, and joined more piping parties even when it meant leaving the nest. This is in contrast to females. It is possible that males were still mate-guarding, for they could still be cuckolded if re-laying was necessary.

In contrast to my findings for the incubation stage, Nol (1984) found no change in the amount of time American Oystercatchers spent piping between prenesting and incubation stages, and still no difference between the sexes, although males chased other oystercatchers more than females did. These observations are consistent with the suggestion that this species nested in an area where few non-breeding oystercatchers posed a threat of cuckoldry or competition. Helbing's (1977) reports for intraspecific aggression during incubation in Black Oystercatchers in California are also in contrast to mine. This population showed a marked increase in intraspecific aggression, particularly for the male, after egg-laying which was maintained after hatching. However, decreased hostility toward conspecifics after egg-laying is common in several monogamous shorebirds (Holmes 1971, Nethersole-Thompson

1973, Gibson 1978, Miller 1979, Howe 1982, Mundahl 1982).

After hatching, females responded to more conspecific intruders, but these levels were still lower than the response by males, which was similar to that during incubation. During incubation, females rarely left the nest to respond to intrusions by conspecifics, and thus the increase following hatching may reflect the release from incubation duties. On the other hand, this increase may be in response to the need to defend chicks from attacks by conspecifics. The gradual decrease in the percentage of time spent piping through the chick rearing stages is in part a reflection of the decrease in the number of intruding conspecifics. It may also be in response to the decrease in the need to defend against cuckoldry and competition. Another consideration may be the decrease in the vulnerability of the chick as it approaches independence.

In contrast to my findings for Black Oystercatchers, Nol (1984) recorded substantial increases, particularly for the male, in the level of intraspecific aggression of American Oystercatchers following hatching. Gibson (1978) reported a similar pattern for avocets. Neither of these researchers comment on this increase, which appears to be opposite to what would be expected if intraspecific aggression served primarily to protect mates and territory from conspecifics. However, the increased frequency of agonistic acts by both sexes of several gull species after hatching has been associated with movements of chicks within the territory, the presence and movement of chicks on neighbouring territories, and the corresponding movements of adults related to feeding chicks and foraging (Hunt and Hunt 1976, Burger 1980, Butler and Janes-Butler 1984). It is possible that the increases reported for avocets and American Oystercatchers occur for similar reasons.

Interspecific interactions (HU)

Gull pairs were defending territories and building nests during the oystercatcher prenesting stage. Gulls were therefore close to the nesting oystercatchers throughout the gulls' breeding season, at least until the chicks joined the adults on the foraging ground. Thus, it is likely that the intrusion rate by gulls remained fairly constant over the breeding stages.

Gulls and crows do not pose a threat to adult oystercatchers, and the relatively low levels of hostility toward these species before egg-laying reflect this. However, interspecific aggression during this stage seemed to serve to prevent gulls from nesting close to oystercatcher nests.

As in intraspecific aggression exhibited prior to egg-laying, males were also more aggressive in interactions with other species, mainly because they attacked gulls and crows.

A similar sexual difference in interspecific aggression has been reported for American Oystercatchers (Nol 1984) and Black Oystercatchers elsewhere (Helbing (1977), but not for Blackish Oystercatchers (Nol 1984). Gibson (1978) reported that male and female avocets exhibited similar levels of aggression (diversionary behaviour) before egg-laying. The lack of sexual difference in interspecific aggression may be a reflection of the lower frequency of contact with other species since both Gibson and Nol report that avocets and Blackish Oystercatchers chased other species at lower frequencies than oystercatchers did in this study.

Both sexes of Black Oystercatcher, but especially females, sharply increased their level of aggression following hatching, primarily due to the increase in their interactions with gulls. This was not due to an increase in the intrusion rate by gulls, but could be due to the increased vulnerability of mobile chicks in comparison to eggs, or alternatively, to the increased relative value of chicks compared to eggs (Trivers 1972). Interactions with gulls decreased as the chicks grew older and moved away from the nest, although levels of interspecific aggression remained higher than during prenesting and incubation stages. Gulls posed a threat to oystercatcher chicks until the chicks could fly.

After hatching, American Oystercatchers (Nol 1984) and Black Oystercatchers elsewhere (Helbing 1977) also showed a marked increase in the frequency with which they chased other species, but the increase was not as great as shown by Black Oystercatchers on Cleland Island. Nol (1984) considered only one chick rearing stage and did not indicate its duration. It is also possible that the intrusion rate by other species was lower on Nol's and Helbing's study sites than it was on Cleland Island, as suggested above. The pattern of a decrease then increase in interspecific aggression has been reported for the Variable Oystercatcher (Jones 1979) and several other monogamous shorebirds (Drury 1961, Jehl 1973, Mundahl 1982).

Gibson (1978) also reported, for avocets, a similar pattern of low levels of interspecific aggression (diversionary behaviour) before hatching followed by a marked increase after hatching, with females increasing aggression more than males.

Parental Care (PC)

Nest Build (NB)

Behaviours used to build nests (BT and NP) appear to be highly stereotyped within the shorebird group (Makkink 1942, Harrison 1967, Hamilton 1975, Cairns 1982).

Male Black Oystercatchers took a dominant role in nest building by initiating most bouts of nest building and usually moving to another nest site followed by the female. However, the female seemed to decide ultimately which nest-scrape would be used. Nol (1984) found that the male Blackish Oystercatchers also took a dominant role in nest building. The pattern of male-dominated nest building is also reported for avocets (Gibson 1978) and other monogamous breeding shorebirds (Holmes 1966, 1973, Jehl 1973, Nethersole-Thompson and Nethersole-Thompson 1979, Ashkenazie and Safriel 1979b, Cairns 1982, Mundahl 1982) and some gull species (Fordham 1964, Bernstein and Maxson 1984). Several of these authors have commented that the birds could probably build an adequate nest in a much shorter time, and speculate that the construction of numerous scrapes over a long period of time served to strengthen the pair bond. The observation in this study that nest building usually occurred only when both pair members were present and close to the nest supports this suggestion.

Black Oystercatchers frequently engaged in bouts of BT as they left the nest when relieved of incubation duty. The nest was maintained throughout the incubation period, in this way, although this behaviour may still be considered a courtship display.

Black Oystercatchers infrequently engaged in bouts of BT during intense interactions with conspecifics during all stages of the breeding cycle. These appear similar to "false-feeding" described for similar situations in the European Oystercatcher (Makkink 1942) and probably represent displacement behaviour.

Incubate (INC)

The irregular covering of the incomplete clutch, seen in the Black Oystercatcher, is not quantified in many studies. Harris (1970) mentions that the European Oystercatcher did not cover the incomplete clutch and that this contributed to the observed predation. Nol (1984) reports that the American Oystercatcher did not commence incubating until the second egg was laid. Covering of the incomplete clutch has been documented in avocets (Gibson 1978, Sordahl 1980) and other shorebird species (Norton 1972, Maxson and Oring 1980, Mundahl 1982, Bergstrom 1982, Miller 1983) but documented as not occurring in others (Holmes 1973). Such covering is often reported in association with adverse conditions such as extremes in temperature or threat of predation. For Black Oystercatchers in this study, covering the incomplete clutch could be a consequence of predation pressure by gulls and crows, and would also explain the almost continual guarding, not seen in species that nest in relative isolation from potential predators.

Although the eggs were covered, incubation was probably not effective as the eggs rarely hatched in the order they were laid (L'Hyver pers. comm.). Effective incubation would lead to asynchronous hatching which is highly detrimental to nidifugous young (Soikkeli 1967, Vince 1966, Norton 1972, Ashkenazie and Safriel 1979b).

Although irregular covering of the incomplete clutch has been documented for sandpipers and plovers, usually no mention is made of the sex of the bird involved. However, those that do mention the sex, report that males usually do the egg-covering (Miller 1977, Gibson 1978, Ashkenazie and Safriel 1979b, Mundahl 1982, Bergstrom 1982). Females probably need to recover from egg laying by spending more time foraging and resting (standing and sitting), as female oystercatchers did in this study (Appendix 3.2a), a situation also reported for female avocets (Gibson 1978) and Killdeer (*Charadrius vociferus*, Mundahl 1982). This would take the females away from the nest which would quickly be preyed upon by gulls or crows if left unguarded.

Continuous incubation of the complete clutch is typical of monogamous shorebirds, even though many species breed in areas where ambient temperatures eliminate the need to keep the eggs warm. However, continuous incubation is probably necessary to ensure successful hatching in areas with high predation pressure. Indeed, unattended oystercatcher eggs on Cleland Island were quickly taken by gulls or crows.

Sharing of incubation by pair members typifies monogamously breeding shorebirds. I found no evidence for Black Oystercatchers (nor did Helbing (1977)) for the same species, nor did Nol (1984) for American Oystercatchers) of a diel pattern in the sharing of incubation, as exhibited by many monogamous shorebirds (Soikkeli 1967, Parmelee *et al.* 1968, Jehl 1971, 1973, Holmes 1971, 1973, Norton 1972, Nakazawa 1979, Mundahl 1982, Howe 1982, Miller 1985). These researchers report a general trend of male incubation by day and female by night. Webster (1941) stated that male and female Black Oystercatchers took turns incubating over the tidal cycle, and changed approximately every twelve hours. However, this conclusion was based on only a few observations and I concur with Hartwick (1974) that it is probably wrong.

Most information on the relative participation of the sexes is qualitative, or based on a single estimate over the entire incubation period. Most of these suggest the females incubate more then their mates. Qualitative studies of oystercatchers indicate that both sexes incubate (Buxton 1939, Webster 1941, Hall 1959). Helbing (1977) reported that male Black Oystercatchers in California provided approximately 40 per cent of the incubation on all observation days. Nol (1984) reported that American Oystercatcher males incubated 18 per cent less than did females, but she did not examine changes in the relative participation of the sexes over the incubation period. Gibson (1971, 1978) reported that male avocets dominated incubation during the first eight days and the females for the last 16 days. However, these estimates were made on the basis of only four pairs, which showed much interpair variability. At least one of these three pairs exhibited a pattern of male-dominated incubation in the last week of the incubation period. Studies on larids indicate that females incubate more than males (Pierotti 1981, Butler and Janes-Butler 1983, Maxson and Bernstein 1984), but in all of these, only one estimate is given for the entire incubation period and the data were not examined for changes over the breeding season.

A gradual increase in male participation in incubation as it proceeds, as seen in this study, has also been noted for several other monogamous shorebirds (Holmes 1966 Soikkeli 1967, Ashkenazie and Safriel 1979b, Miller 1985) but also has been reported as not occurring in others (Jehl 1973, Howe 1982). Since the conclusions in the latter two cases were based on nest checks, it is possible that subtle changes in relative participation may have gone undetected.

Greater investment by females in gamete production is assumed to predispose them to greater commitment to the eggs; thus, females are predicted to incubate more than males (Trivers 1972). However, this notion of greater investment by females at the onset of incubation has been disputed (Gladstone 1979, Montevecchi and Porter 1980, Burger 1981, Werschkul 1982). These authors suggest that male contribution through territorial defence and nest building results in more equal cumulative investment at this point. Indeed, in this study, males were the more aggressive and alert sex in intraspecific interactions. Also, during the incubation stages, males frequently left the nest in response to the approach of a conspecific. In these circumstances their mates usually took over incubation even if the male returned to the vicinity of the nest. Females appeared to be more reluctant to leave the nest. These observations suggest that greater participation in incubation by females after laying, may reflect their response to the need to keep the eggs covered when their mates leave the nest. This is exemplified by the interpair variability in the pattern of sharing of incubation. The increase in male participation in incubation as it proceeds may be a reflection of the increase in value of the egg to the male in terms of past investment (Trivers 1972) or future expectations (Dawkins and Carlisle 1976). There is also the consideration of the reduction of alternative possibilities of the male increasing its fitness through extrapair copulations with the advancement of the breeding season (Maynard Smith 1977). Thus, it may not be coincidental that increased participation in incubation by male oystercatchers, and other monogamously breeding shorebirds, occurs toward the end of the incubation period, when most territory-holding females are sitting on eggs and unavailable.

Incubation bouts by Black Oystercatchers appear to be much shorter than those of other species, corresponding to the absence of a predictable diel incubation pattern. Ashkenazie and Safriel (1979a) report that Semipalmated Sandpiper bout durations are 3-5 hr at the beginning of incubation and increase to 14 hr at the end. Incubation bouts by the more closely related avocets and Black-necked Stilts (*Himantopus mexicanus*) are more similar to those I found for the Black Oystercatcher. To facilitate comparisons, average bout durations, using the bout duration rather than the individual as the sampling unit, are presented in Table 10.

Table 10: Comparison of the mean incubation bout durations (in minutes) of male and female Black Oystercatchers, American Avocets and Black-necked Stilts; considering the incubation bout as the sample.

Species	female		male		Source
	n	$\bar{x}$	n	$\bar{x}$	
Black Oystercatcher	147	57.7	141	39.2	this study
	-	74.0	-	56.0	Helbing 1977
American Avocet	18	64.3	26	87.6	Hamilton 1975
	-	52.2	-	38.0	Gibson 1971
Black-necked Stilt	10	82.0	11	64.6	Hamilton 1975

Incubation bouts are influenced by temperature (e.g. Caldwell and Cornwell 1975, Haftorn 1983). However, I do not feel that temperature greatly affected the duration of incubation bouts in this study. Incubating oystercatchers sometimes responded to high temperatures by standing over the eggs. Such breaks in incubation were not considered to be a bout termination unless the mate took over incubation duties (see Methods section).

Considering the context of departures from the nest, it appears that Black Oystercatchers on Cleland Island show no fixed pattern of nest relief beyond that of keeping the eggs covered (supported by the interpair variability discussed below). The irregular pattern of nest relief may be influenced in part by the coastal habitat where foraging opportunities are also variable since they are controlled by the tide. Another contributing factor was probably the presence of large numbers of gulls and non-breeding oystercatchers, whose close proximity often resulted in the incubating oystercatcher leaving the nest. It would be necessary to compare bout duration of oystercatchers nesting in more typical isolated situations to establish representative bout durations of this species. However, the American Oystercatcher is also reported to have relatively short incubation bouts of approximately two hours for the female and shorter for the male (Nol pers. comm.), suggesting that short incubation bouts are a trend among haematopodids.

Few studies of incubation behaviour report sexual differences in bout durations. Buxton (1939) noted that male European Oystercatchers appeared to be more nervous and incubated for shorter periods of time and Nol (pers. comm.) reports that, qualitatively, male American Oystercatchers behave similarly. Avocet and stilt males also incubate for briefer periods than their mate (Table 10). Male Black Oystercatchers frequently left the nest in response to the approach of a conspecific or potential predator, which often resulted in short incubation bouts. Females appeared more reluctant to leave the nest, which probably contributed to their longer bout durations.

The gradual increase in duration of incubation bouts with the advance of the incubation period, exhibited by both sexes of Black Oystercatcher, is also known for Semipalmated Sandpipers (Ashkenazie and Safriel 1979a) and several gull species (Drent 1970, Bernstein and Maxson 1984). The increased participation previously noted for males of other monogamous shorebirds over the breeding season is probably the result of an increase in incubation-bout duration. Ashkenazie and Safriel (1979b) concluded that the shift was not associated with energetic considerations because male and female Semipalmated Sandpipers had similar energetic requirements throughout the incubation period. Norton (1972) suggested that, since embryos increased in sensitivity to cold with age, increasing the length of incubation turns would reduce the amount of time the eggs were exposed. Increased bout duration would also decrease the number of times and the amount of time the eggs were exposed to predators. Related to this is the increase in the value of the eggs with the advancement of the incubation period both in terms of past investment (Trivers 1972) and the decrease in the possibility of egg replacement with the progression of the breeding season.

Behind the general trend in relative participation is considerable interpair variability in the sharing of incubation responsibilities. In experimental analysis of factors influencing the timing of incubation bouts by Ring Doves, Wallman *et al.* (1979) and Ball and Silver (1983) found a similar pattern of a basic trend in the pattern among pairs, but also found cooperative interaction between pair members in the sharing of incubation that was pair-specific. The extremes in participation by members of Prb and CB pairs suggest that the contribution of an individual toward incubation is flexible and is adjusted to its mate's contribution. The fact that both these pairs lost their chicks at hatching may be an indication that these extreme situations do not ensure reproductive success. However, two of the remaining pairs exhibiting more 'normal' participation were also unsuccessful. Clearly more data are required before the meaning of this flexibility can be interpreted accurately.

Brood (BRO), forage for chick (FFC), and feed chick (FC)

Hatching and early chick-rearing stages are critical periods when chicks are most susceptible to mortality (pers. obs., Soikkeli 1967). Black Oystercatcher chicks were brooded almost continuously during the daytime of the first few days after hatching and thereafter brooding appeared to be associated with low temperatures. I saw no brooding of chicks older than 21 days. Helbing (1977) reported similar findings in Black Oystercatchers breeding in California. Nol (1984) reported that American Oystercatchers brooded for only 11 per cent of the day. These estimates may reflect the higher temperatures in Virginia or the relatively low predation pressure there, both reducing the necessity to brood. However, it is more likely that the estimates were made several days after hatching when chicks did not require as much brooding. Unfortunately, Nol does not provide details of the timing of sampling throughout the breeding season, and therefore the effects of different temperatures and predation pressure cannot be considered.

Both sexes brooded, but in both the Black (this study and Helbing 1977) and American Oystercatcher (Nol 1984), the female did most of it. Brooding by the female leaves the male, which is more vigilant and aggressive, more time to defend the brood, female and territory. Gibson (1978) and Sordhal (1980) report that both sexes of avocet and stilt brood, but these authors do not mention sexual differences. Since both species are difficult to observe once they leave the nest, it is possible for this sexual difference to go unnoticed. Sordhal (1980) reported that, after approximately two weeks, one or both parent avocets sometimes deserted the brood and, when one adult deserted, it was usually the female.

As previously mentioned, estimates for FC and FFC are approximate because of the difficulty of observing these behaviours. However, I feel that the trends in relative participation of the sexes indicated are real.

Male oystercatchers tended to feed and forage for chicks more than did their mates in the period during which chicks were brooded (Stage IVa and IV). Female participation in brooding probably resulted in almost equal participation in chick-rearing during these stages. Once females were freed from brooding duties, the sexes tended to participate equally in feeding and foraging for the chicks. In addition, males and females spent similar amounts of time in proximity to the chicks.

In contrast to this, Helbing (1977) reported that, in one pair, the chicks constantly accompanied the female. Helbing (1977) also reported that females fed their chicks more often than did males (41% males, females 59%) and that there was a sexual difference in the species of invertebrate fed to the chicks. However, he does not report the contribution of each sex in terms of size of the item fed to the chicks which, as previously discussed, may be the more important feature. There were suggestions, in this study, that males of some pairs fed larger items to chicks and accompanied them alone on off-island foraging trips, leaving the female on the territory. However, these data are limited and difficult to obtain. More information is required to verify these trends before any conclusion can be drawn. However, these differences are possible, since sexual differences were found in the items that African Black Oystercatcher (*H. moquini*) fed to their chicks (Hockey and Underhill 1984) and Pierotti (1981) found that male Western Gulls (*L. occidentalis*) brought back heavier loads of fish to their chicks.

As the chicks grew, there was a corresponding increase in the time the adults spent foraging for them. The gradual decrease, observed toward fledging, may be due in part to the chicks foraging for themselves; alternatively, the parents may be attempting to force the chicks to forage for themselves (Trivers 1974).

Most other studies of monogamous shorebirds also find that young broods are attended by both sexes. However, it is usually reported that the increased participation by males in incubation continues after hatching and, in most monogamous shorebirds, shortly after hatching, females desert the male and the brood (review by Miller 1985). The protracted and apparently equal participation by male and female oystercatchers in brood attendance is undoubtedly associated with their unusual foraging and chick-feeding behaviour. Oystercatcher chicks do not attain the skills necessary to forage for themselves until after fledging (> 40 days old, Norton-Griffiths 1969). It is improbable that one adult oystercatcher could provide enough food to sustain the chicks for this period of time. Indirect evidence for this comes from the observation that, even with two adults feeding the brood, some chicks apparently die of starvation (pers. obs., Groves 1984).

Role differentiation in the Black Oystercatcher: summary and concluding comments

Biparental care is undoubtedly essential to the reproductive success of oystercatchers. However, there were recognizable differences in the behaviour of male and female oystercatchers, many of which were consistent with predictions made in relation to the different tactics each sex follows to maximize reproductive success.

Although oystercatchers tend to mate monogamously for life, thus eliminating repeated mate selection with special advertising displays, mates must be defended. The threat of cuckoldry is greatest for males since it may go undetected and the male would waste investment raising someone else's offspring. Females are expected to actively defend their mates from potential competitors when paternal care is necessary for her reproductive success. In response to these threats, both male and female oystercatcher were more aggressive toward conspecifics prior to egg-laying when the threat of cuckoldry is greatest, and males were more aggressive than females.

Female oystercatchers spent more time feeding during the prenesting stage than males did, presumably due to egg production. During this period of high female metabolic cost, males assumed the role of nest-builder and territory defender. Males also assumed the dominant early-incubaion role while their mates presumably recouped energy expended in producing eggs. Egg covering was undoubtedly necessary on Cleland Island where unattended eggs were quickly eaten by crows or gulls.

After egg-laying, females tended to dominate incubation; however, there was no difference in the amount of time each sex spent within six meters of the nest. Males appeared to take on a guarding role, guarding the female and eggs from potential predators, and were also alert for the approach of conspecifics, which still posed the threat of cuckoldry should re-laying have become necessary. Alternatively, the males' behaviour may reflect a trade-off between his two options for maximizing reproductive success. In situations that require large amounts of paternal attention, the male's best chances for reproductive success are within the pair bond, but he should still not pass up the opportunity to inseminate additional females. Thus, it may not be coincidental that the increase in participation in incubation, an activity that renders it difficult to respond to solicitous females, occurred late in the incubation period when most females were sitting on eggs and unavailable, or with diminishment of the chances of success with the advancement of the breeding season.

Females dominated brooding, but males assumed the role of provider for the chicks during this period. After the female was freed from brooding duties, the sexes participated almost equally in chick feeding and care. This was exemplified by the observation that there was no sexual difference in the amount of time spent close to the chicks. Both parents continued to attend and feed the chicks at least until the chicks could fly.

As discussed previously, there are different costs associated with these different forms of parental care, many of which are not additive, thus making it difficult to measure the relative amounts of investment. However, even though role differentiation occurred in Black Oystercatchers, it appears that parental investment is equalized by each sex over a given breeding season. In birds such as oystercatchers, which remain paired for more than one season, the tactic of each partner's involvement in parental behaviour within any one breeding season is unlikely to be purely selfish, since the condition of the mate in following seasons will influence the individual's own reproductive success. This was exemplified by the cooperation between pair members which was pair-specific.

Parental behaviour in the Black Oystercatcher: concluding comments

Biparental care is attributed to a considerable demand for parental care by both parents (Emlen and Oring 1977). Correspondingly, differences in the quality and quantity of parental care should be influenced by the demand for it. However, it is interesting to note how similar the pattern of parental behaviour is when comparisons are made among oystercatcher species that breed at different latitudes with corresponding differences in weather (e.g. Black Oystercatcher, B. C., Canada, 49° 10'N 126° 505'W; American Oystercatcher, Virginia, U. S. A., 37° 55'N 75° 23'W; and Blackish Oystercatcher, Punta Tombo, Argentina, 44° 02'S 65° 12'W). Parental behaviour in oystercatchers includes: biparental incubation; no diel pattern in the sharing of incubation; short incubation bouts; and female-dominated brooding. These characteristics are qualitatively and quantitatively more similar to those of members of the closely related Recurvivostridae than to those of members of the more distantly related Scolopacidae. Parental care in monogamously breeding scolopacids is summarized as including: biparental care in incubation and care of the brood; males asssuming an increased role late in the nesting cycle; diel rhythm in sharing of incubation; and dominant male role in brood care (Miller 1985). Comparison among Haematopodidae, Recurvivostridae and Scolopacidae should provide insight into the adaptive significance of these differences (Walters 1984, Fitzpatrick 1985).

Members of the Recurvivostridae and Haematopodidae are relatively large, long-lived shorebirds that exhibit long-term fidelity to mate and territory. Also, oystercatchers are mostly non-migratory. In these characteristics, they contrast to varying degrees with many scolopacids. The differences in parental behaviour between these groups appear to be related largely to these contrasts.

With regard to diel sharing of incubation by male and female Killdeer, Mundahl (1977) proposed that the risk of predation to the incubating bird might be greater at night than during the day and that this investment by the male could thus balance the investment by the female in egg production. It is unlikely that potential predation would influence incubation patterns of oystercatchers, since they have relatively few predators. Miller (1977) suggested that this diel rhythm prevails to lessen the energetic strain of incubating during the cool night on the smaller males, and to allow females to recoup their investment in egg production by foraging when temperatures are higher and invertebrates more active during the day. The absence of such a diel rhythm in oystercatchers may in part be a reflection of the larger relative size of oystercatchers breeding in lower latitudes than many of the species mentioned above. Also, food availability on Cleland Island is discontinuous, dependent on the tidal cycle rather than on the diel cycle and related temperature changes. However, Nol (1984) also found no diel incubation cycle in an area where food availability was continuous, suggesting that this trait is conservative within this genus.

The shorter incubation bouts exhibited by oystercatchers and recurvivostrids are no doubt related to their lack of diel sharing of incubation, but also may be attributed to other factors. There appears to be no increase in metabolic cost associated with incubation, but incubating birds cannot forage, which may cause energetic stress. The length of an incubation bout is particularly important to birds that breed in intertidal areas where foraging opportunities are not continuous. A bird that incubated through a low tide period would be unable to forage when relieved at high tide. This stress could be reduced by short incubation bouts, allowing both birds the opportunity to forage at low tide.

Long incubation bouts in scolopacids and short ones in oystercatchers and recurvivostrids may be related to their specific anti-predator behaviour. Most adult scolopacids are susceptible to predation on the nest. Most of these birds conceal their nests and their anti-predator behaviour includes sitting tight or early surreptitious departure at the approach of a predator. Short incubation bouts, accompanied by change-overs in the incubating birds, would advertise the nest's location and attract potential predators. In contrast to most sandpipers, oystercatchers are conspicuous on their nest and use direct attacks as the main form of anti-predator behaviour (Sordahl 1981). Thus, repeated change-overs of incubation do not have the same deleterious effect.

Two ideas have been proposed to explain desertion by one sex following hatching as seen in many monogamously breeding scolopacids. Several authors view desertion by one sex as a mechanism for reducing intra- and interspecific competition for food. This applies mainly to shorebirds that rely on emerging insects for food, rather than oystercatchers, since their food supply is relatively stable over the breeding season (Holmes 1968, Pitelka *et al.* 1974). Others view desertion by the female as a stress-reducing mechanism in migratory shorebirds since females are usually assumed to be strained energetically more than males are by the high energy requirements of reproduction (Ashkenazie and Safriel 1979b, Lenington 1980). Most oystercatchers are non-migratory and are therefore not stressed by this in addition to the activities of the breeding season. This perhaps eliminates the need for desertion.

In summary, the pattern of role differentiation and the parental behaviour exhibited by oystercatchers appears to be related to the relatively large size of oystercatchers, their longevity, long term mate fidelity, and sedentary life style.

VI BIBLIOGRAPHY

Abramson, M. 1979. Vigilance as a factor influencing flock formation among curlews (*Numenius arquata*). Ibis 121:213-216.

Andersson, M., C. G. Wiklund and M. Rundgren. 1980. Parental defense of offspring: A model and an example. Anim. Behav. 25:536-542.

Ashkenazie, S. and U. N. Safriel. 1979a. Breeding cycle and behavior of the Semipalmated Sandpiper at Barrow, Alaska. Auk 96:56-67.

-------------------------------- 1979b. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. Ecology 60:783-799.

Baker, A. J. 1974. Criteria for aging and sexing New Zealand Oystercatchers. N. Z. J. Mar. Freshw. Res. 8:211-221.

------------ 1975. Lipid levels in the South Island Pied Oystercatcher (*Haematopus ostralegus finschi*). N. Z. Jour. of Zool. 2:425-434.

Ball, G. F. and R. Silver. 1983. Timing of incubation bouts by Ring Dove (*Streptopelia risoria*). J. Comp. Psychol. 97:213-225.

Barash, D. P. 1975. Evolutionary aspects of parental behavior: Distraction behaviour of the Alpine accentor. Wilson Bull. 87:367-373.

------------- 1982. Sociobiology and Behavior Elsevier, New York.

Bergstrom, P. W. 1982. Ecology of incubation in Wilson's Plover (*Charadrius wilsonius*). Ph.D. thesis. University of Chicago.

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

Bray, O. E., J. J. Kennelly, and J. L. Guarina. 1975. Fertility of eggs produced on territories of vasectomized Red-winged Blackbirds. Wilson Bull. 87:187-195.

Burger, J. 1981. Sexual differences in parental activities of breeding Black Skimmmers. Amer. Natur. 117:975-984.

Burger, J. and C. G. Beer. 1975. Territoriality in the Laughing Gull (*L. atricilla*). Behaviour 55:301-320.

Butler, R. G. and S. Janes-Butler. 1983. Sexual differences in the behavior of adult Great Black-backed Gulls (*Larus marinus*) during the pre- and post-hatch periods. Auk 100:63-75.

Buxton, E. J. M. 1939. The breeding of the oystercatcher. Brit. Birds 33:184-193.

Cairns, W. E. 1982. Biology and behavior of breeding Piping Plovers. Wilson Bull. 94:531-545.

Caldwell, P. J. and G. W. Cornwell. 1975. Incubation behavior and temperatures of the Mallard duck. Auk 92:706-731.

Cramp, S. (*ed.*) 1983. Handbook of the birds of Europe, the Middle East, and North Africa. The birds of the western Palearctic. Vol. 3. Waders to gulls. Oxford University Press, Oxford.

Curio, E. 1975. The functional organization of anti-predator behaviour in the Pied Flycatcher. A study of avian visual perception. Anim. Behav. 23:1-115.

Dare, P.J. 1977. Seasonal changes in body-weight of oystercatchers *Haematopus ostralegus*. Ibis 119:494-506.

Dawkins, R. and T. R. Carlisle. 1976. Parental investment and mate desertion: a fallacy. Nature, Lond. 262:131-133.

Dimond, S. J. and J. Lazarus. 1974. The problem of vigilance in animal life. Brain, Behav. Evol. 9:60-79.

Dircksen, R. 1932. Die Biologie des Austernfishers, der Brandseeschwalbe und der Kustenseechwalbe nach Beobachtungen und Untersuchungen auf Horderoog. J. Orn. 80:427-521.

Drent, R. H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Suppl. 17:1-132.

Drury, W. H. Jr. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. Auk 78:176-219.

El-Wailly, A. J. 1966. Energetic requirements for egg-laying and incubation in the Zebra Finch, *Taeniopygia castanotis*. Condor 68:582-594.

Emlen, S. T. and L. W. Oring. 1979. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Erckmann, W. J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypothesis. *In* Social behaviour of female vertebrates. *Edited by* S. K. Wasser. Academic Press, New York. pp. 113-168.

Ericksen, C. J. and P. G. Zenone. 1976. Courtship differences in male Ring Doves: avoidance of cuckoldry. Science 192:1353-1354.

Fagen, R. M. and D. Y. Young. 1978. Temporal patterns of behaviors: durations, intervals, latencies and sequences. *In* Quantitative Ethology. *Edited by* P. W. Colgan. John Wiley and Sons.

Finch, D. M. 1984. Parental expenditure of time and energy in the Abert's Towhee (*Pipilo aberti*). Auk 101:473-486.

Fitzpatrick, J. W. 1981. Search strategies of Tyrant Flycatchers. Anim. Behav. 29:810-821.

--------------- 1985. Scientific collections and the study of ecological morphology. *In* Museum collections: their role and future in biological research. *Edited by* E. H. Miller. Occas. Pap. B. C. Prov. Mus. (Victoria). pp. 195-208.

Fleischer, R. C. 1983. Relationships between tidal oscillations and Ruddy Turnstone flocking, foraging and vigilance behavior. Condor 85:22-29.

Fordham, R. A. 1963. Individual and social behaviour of the Southern Black-backed Gull. Notornis 10:206-222.

French, N. R. 1959. Life history of the Black Rosy Finch. Auk 75:159-180.

Gibson, F. 1971. The breeding biology of the American Avocet in central Oregon. Condor 73:444-454.

---------- 1978. Ecological aspects of the time budget of the American Avocet. Am. Midl. Nat. 99:65-82.

Gladstone, D. 1979. Promiscuity in monogamous colonial birds. Amer. Natur. 114:545-557.

Gochfeld, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. *Edited by* J. Burger and B. Olla. Plenum Press, New York. pp. 289-377.

Gottfried, B. M. 1979. Anti-predator aggression in birds nesting in old field habitats: an experimental analysis. Condor 81:251-257.

Grant, G. S. 1984. Energy cost of incubation to the parent seabird. *In* Seabird Energetics. *Edited by* G. C. Whittow and H. Rahn. Plenum Press, New York. pp. 59-71.

Groves, S. 1982. Aspects of foraging in Black Oystercatchers (Aves: Haematopodidae). Ph. D. Thesis, University of British Columbia, Vancouver B.C.

---------- 1984. Sibling rivalry and chick production in the American Black Oysteratcher. Auk 101:525-531.

Haftorn, S. 1983. Egg temperature during incubation in the Great Tit *Parus major* in relation to ambient temperature, time of day, and other factors. Cinclus 6:22-38.

Hall, K. R. L. 1959. Observations on the nest-sites and nesting behaviour of the Black Oystercatcher *Haematopus moquini* in the Cape Peninsula. Ostrich 30:143-154.

Hamilton, R. B. 1975. Comparative behavior of the American Avocet and the Black-necked Stilt (Recurvivostridae). A. O. U. Ornithol. Monogr. 17:1-98.

Harris, M. P. 1967. The biology of oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. Ibis 109:180-193.

Harris, R. J. 1975. A primer of multivariate statistics. Academic Press, Inc. N. Y.

------------- 1970. Territory limiting the size of the breeding population of the oystercatcher (*Haematopus ostralegus*): A removal experiment. J. Animal Ecol. 39:707-713.

Harrison, C. J. O. 1967. Sideways-throwing and sideways-building in birds. Ibis 109:539-551.

Hartwick, E. B. 1973. Foraging straegy of the Black Oystercatcher. Ph. D. thesis. University of British Columbia, Vancouver, B. C.

--------------- 1974. Breeding ecology of the Black Oystercatcher (*Haematopus bachmani*)). Syesis 7:83-92.

--------------- 1978. The use of feeding areas outside of the territory of breeding Black Oystercatchers. Wilson Bull. 90:650-652.

Hartwick, E. B. and W. Blaylock. 1979. Winter ecology of a Black Oystercatcher population. Studies Avian Biol. 2:207-215.

Helbing, G. L. 1977. Maintenance activities of the Black Oystercatcher, *Haematopus bachmani* Audubon, in Northwestern California. M. Sc. thesis, Humbolt State University, California.

Heppleston, P. B. 1972. The comparative breeding ecology of oystercatchers (*Haematopus ostralegus* L.) in inland and coastal habitats. J. of Animal Ecology 41:23-51.

Heppleston, P. B. and Kerridge, D. F. 1970. Sexing oystercatchers from bill measurements. Bird Study 17:48-49.

Hockey, P. A. P. 1981. Morphometrics and sexing of the African Black Oystercatcher. Ostrich 52:244-247.

Hockey, P. A. R. and L. G. Underhill. 1984. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. S. Afr. J. Zool. 19:1-11.

Holmes, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68:3-46.

------------- 1971. Density, habitat, and the mating system of the Western sandpiper (*Calidris mauri*). Oecologia 7:191-208.

------------- 1973. Social behavior of breeding Western Sandpipers *Calidris mauri*. Ibis 115:107-123.

------------- 1968. Food overlap among coexisting sandpipers on nothern Alaskan tundra. Systematic Zoology 17:305-318.

Howe, H. F. 1979. Evolutionary aspects of parental care in the Common Grackle, (*Quiscalus quiscula* L.). Evolution 33:41-51.

Howe, M. A. 1982. Social organization in a nesting population of Eastern Willets (*Catoptrophorus semipalmatus*). Auk 99:88-102.

Hull, C. and N. Nie 1979. (*Eds.*) SPSS Update: New procedures and facilities for Releases 7 and 8. McGraw-Hill Book Co., New York

Hunt, G. L. and M. W. Hunt. 1977. Female-female pairing in Western Gulls (*Larus occidentalis*) in southern California. Science 196:1466-1467.

Huxley, J. S. and F. A. Montegue. 1925. Studies on the courtship and sexual life of birds V. The oystercatcher (*Haematopus ostralegus*) Ibis 12:868-897.

Jehl, J. R. 1971. Patterns of hatching success in subarctic birds. Ecology 52:169-173.

----------- 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bull. 85:115-147.

Joyner. S. P. 1983. (*Ed.*) SUGI Supplemental Library User's Guide, 1983 Edition. SAS Institute Inc. Cary, N.C.

Jones, A. 1979. Notes on the behaviour of Variable Oysteratchers. Notornis 26:47-52.

Knapton, R. W. 1985. Parental inestment: the problem of currency. Can. J. Zool. 62:2673-2674.

Kruskal, J. B. and M. Wish. 1978. Multidimensional Scaling. Sage University Paper Series on Quantitative Applications in the Social Sciences, series no. 07-011. Beverly Hills and London: Sage Publications.

Lazarus, J. and I. R. Inglis. 1978. The breeding behaviour of the pink-footed goose: parental care and vigilant behaviour during the fledging period. Behaviour 665:62-88.

Lenington, S. 1980. Bi-parental care in the Killdeer: an adaptive hypothesis. Wilson Bull. 92:8-20.

Lenington, S. 1984. The evolution of polyandry in shorebirds. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. *Edited by* J. Burger and B. Olla. Plenum Press, New York. pp. 243-287.

Lind, H. 1965. Parental feeding in the oystercatcher (*Haematopus o. ostralegus*). Dansk Orn. Foren. Tidsskr. 59:1-31.

Makkink, G. F. 1942. Contribution to the knowledge of the behaviour of the oystercatcher. Ardea 31:23-74.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25:1-9.

Maxson, S. J. and N. P. Bernstein. 1984. Breeding season time budget of the Southern Black-backed Gull in Antarctica. Condor 86:401-409.

Maxson, S. J. and L. W. Oring. 1980. Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. Behaviour 74:200-263.

Mercer, A. J. 1968. Individual weight changes in breeding oystercatchers. Bird Study 15:93-98.

Metcalfe, N. B. 1984a. The effect of mixed-species flocking on the vigilance of shorebirds: who do they trust? Anim. Behav. 32:986-993.

--------------- 1984b. The effects of habitat on the vigilance of shorebirds: is visibility important? Anim. Behav. 32:981-986.

Metcalfe, N. B. and R. W. Furness 1984. Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. Behav. Ecol. Sociobiol. 15:203-206.

Miller, E. H. 1977. Breeding biology of the Least Sandpiper, *Calidris minutilla* (Vieill.) on Sable Island, Nova Scotia. Ph. D. thesis, Dalhousie University, Halifax, N. S.

------------- 1979. Functions of display flights by males of the Least Sandpiper *Calidris minutilla* on Sable Island, Nova Scotia. Can. J. Zool. 57:876-893.

------------- 1983. Habitat and breeding cycle of the Least Sandpiper (*Calidris minutilla*) on Sable Island, Nova Scotia. Can. J. Zool. 61:2880-2898.

------------- 1985. Parental behavior in the Least Sandpiper (*Calidrius minutilla*). Can. J. Zool. 63:1593-1601.

Miller, E. H. and A. J. Baker 1980. Displays of the Magellanic Oystercatcher (*Haematopus leucopodus*). Wilson Bull. 92:149-168.

Montevecchi, W. A. amd J. M. Porter 1980. Parental investments of seabirds at the breeding area with emphasis on Northern Gannet *Morus bassanus*. *In* Behavior of Marine Animals, Vol. 4. *Edited by* J. Burger, B. Olla and H. Winn. Plenum Press. pp. 323-365.

Mundahl, J. T. 1977 Role specialization in the parental and territorial behavior of the Killdeer (*Charadrius vociferus*). M. Sc. Thesis Utah State University, Logan, Utah.

-------------- 1982. Role specialization in the parental and territorial behavior of the Killdeer. Wilson Bull. 94:515-530.

Nakazawa, R. 1979. [Incubation behaviour of the Kentish Plover, *Charadrius alexandrinus* with special reference to the share of sexes and of effect ground surface temperature.] (In Japanese) Misc. Rep. Yamashina Inst. for Ornithol. 11:54-63.

Nethersole-Thompson, D. 1973. The Dotterel. Collins, London.

Nethersole-Thompson, D. and M. Nethersole-Thompson. 1979. Greenshanks. T. and A. D. Poyser, Berkhamsted.

Nol, E. 1984. Reproductive strategies in the oystercatchers (Aves: Haematopodidae). Ph.D. Thesis University of Toronto, Toronto, Ontario.

Norton, D. W. 1972. Incubation schedules of four species of calidridine sandpiper at Barrow, Alaska. Condor 74:164-176.

Norton-Griffiths, M. 1969. The organization, control and development of parental feeding in the oystercatcher (*Haematopus ostralegus*). Behaviour 34:55-114.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Amer. Natur. 103:589-603.

Oring, L. W. and D. B. Lank 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. *Edited by* J. Burger and B. Olla. Plenum Press, New York. pp. 125-147.

Parmalee, D. F., D. W. Greiner, and W. D. Graul. 1968. Summer schedule and breeding biology of the White-rumped Sandpiper in the central Canandian Arctic. Wilson Bull. 80:1-29.

Pierotti, R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. Auk 98:532-549.

Pitelka, F. A., R. T. Holmes and S. F. MacLean, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. Amer. Zool. 14:185-204.

Power, H. W. 1980. Experiments on cuckoldry in the Mountain Bluebird. Amer. Natur. 116:705-709.

Ray, A. A. 1982. (*Ed.*) User's Guide: Basics, and User's Guide: Statisitics, 1982 Edition. SAS Institute Inc. Cary, N. C.

Robertson, R. J. and G. C. Biermann. 1979. Parental investment; strategies determined by expected benefits. Z. Tierpsychol. 50:124-128.

Soikkeli, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4:158-198.

Sokal, R. and F. J. Rohlf 1981. Biometry. W. H. Freeman and Company. New York.

Sordahl, T. A. 1980. Antipredator behavior and parental care in the American Avocet and Black-necked Stilt (Aves: Recurvirostridae) Ph. D. thesis, Utah State University, Logan, Utah.

-------------- 1981. Predator-mobbing behaviour in the shorebirds of North America. Wader Study Group Bull.

Southern, L. K. 1981. Sex-related differences in territorial aggression by Ring-billed Gulls. Auk 98:179-181.

Trivers, P. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man 1871-1971. *Edited by* B. G. Campbell. Chicago Aldine-Atherton. pp. 136-179.

----------- 1974. Parent-offspring conflict. Amer. Zool. 14:249-264.

van Rhijn, J. 1984. Phylogenetical constraints in the evolution of parental care strategies in birds. Neth. J. Zool. 34:103-122.

Vince, M. A. 1966. Artificial acceleration of hatching quail embryos. Anim. Behav. 14:389-394.

Wallman, J. M., M. Grabon, R. Silver. 1979. What determines the pattern of sharing of incubation and brooding in Ring Doves? J. Comp. Physiol. Psychol. 93:481-492.

Walsberg, G. E. and J. R. King. 1978. The energetic consequences of incubation for two passerine species. Auk 95:644-655.

Walters, J. R. 1982. Parental behavior in lapwings (Charadriidae) and its relationships with clutch size and mating systems. Evolution 36:1030-1040.

-------------- 1984. The evolution of parental behaviour and clutch size in shorebirds. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. *Edited by* J. Burger and B. Olla. Plenum Press, New York. pp. 243-287.

Weatherhead, P. J. 1979. Do Savannah Sparrows commit the concorde fallacy? Behav. Ecol. Sociobiol. 5:373-381.

Webster, J. D. 1941. The breeding of the Black Oystercatcher. Wilson Bull. 53:141-156.

Werschkul, D. F. 1982. Parental investment; influence of nest guarding by male Little Blue Herons, *Florida caerulea*. Ibis 124: 343-347.

West, G. C. 1968. Bioenergetics of captive Willow Ptarmigan under natural conditions. Ecology 49: 1036-1045.

Wiley, R. H. and S. A. Hartnett. 1980. Mechanisms of spacing in groups of juncos: measurements of behavioural tendencies in social situations. Anim. Behav. 28:1005-1016.

Williams, G. C. 1966. Adaptation and natural selection. University Press, Princeton.

Wilson, E. O. 1975. Sociobiology, the New Sythesis. Harvard University Press, Cambridge, Mass.

Wittenberger, J. F. 1982. Factors affecting how male and female bobolink apportion parental investment. Condor 84:22-39.

VII APPENDICES

Appendix 1: Sheet used for data collection.

CLELAND ISLAND 1983

DATE
START
END

WEATHER

TIME	SEX	LOC	BEHAV	COMMENTS

Appendix 2: Number of hours of observation for each of thirteen pairs of Black Oystercatchers in 1983. F=female, M=male, T=total.

	Stage		Pair Name													
			CP	PrA	CB	PrB	JS	FC	N31	N22	N41	N55	AI	PB	GR	Total Time
I	Prenest	F	35.7	20.0	24.9	16.7	46.7									114.1
		M	34.1	19.4	26.3	16.0	45.2									141.2
		T	43.3	29.2	27.9	25.4	56.8									182.7
IIa	Egg	F					10.8	15.6								26.5
	Laying	M					10.9	15.8								26.7
		T					11.5	16.7								28.3
II	Incubation	F			24.2	28.2	24.7	14.4	13.0				12.1			116.8
	(day 2-13)	M			24.7	26.0	25.4	13.9	12.3				9.8			112.2
		T			27.8	29.2	26.2	14.9	13.8				15.4			127.4
III	Incubation	F			25.8	25.2	21.4	29.1	13.2				19.4			134.0
	(>13 days)	M			24.7	27.3	26.2	28.9	13.3				18.0			138.4
		T			29.4	30.2	28.4	31.0	15.1				29.4			162.5
IVa	Hatching	F					12.8		13.0							25.9
		M					13.5		15.5							28.9
		T					14.9		17.6							32.5
IV	Chick	F			12.8		13.8				11.4		11.4			49.4
	Rearing	M			13.1		13.3				12.1		11.8			50.4
	(day 2-10)	T			15.1		14.7				13.8		14.4			57.8
V	Chick	F					41.5			13.9	13.5	10.5	20.1	17.4	10.2	127.2
	Rearing	M					40.3			13.7	12.8	9.8	18.0	17.6	9.9	122.1
	(day 11-30)	T					43.9			14.0	14.6	11.3	27.6	26.4	14.9	152.8
VI	Chick	F					47.7			21.3	11.2	12.1	30.3		18.5	141.1
	Rearing	M					42.9			21.1	12.2	12.0	25.6		18.4	132.3
	(>30 days)	T					55.7			24.5	14.7	13.1	41.0		25.7	174.8

Appendix 3.1: Percent time males and females of five pairs of oystercatchers spent in behaviours during Stage I; Prenesting.

	Behaviour																	
Pair	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	NP	OT	COP
females																		
JS	29.9	42.1	12.1	10.2	0.8	8.1	0.9	0.1	17.2	0.5	1.6	.00	.01	.01	4.20	.13	16.0	.08
PrB	17.2	30.9	27.2	10.3	5.5	1.4	1.8	0.7	14.3	1.1	0.2	.32	.15	.15	.	.	14.9	.06
CP	50.4	55.3	11.2	11.6	2.3	6.5	1.0	0.1	5.6	1.1	0.8	.00	.00	0	1.30	.04	1.5	.
PrA	11.7	39.3	15.2	8.1	10.1	8.7	0.3	0.0	16.2	2.0	0.0	.00	.00	0	0.48	.01	30.6	.04
CB	50.5	55.0	19.8	0.3	6.1	7.3	0.3	0.4	5.9	1.0	1.5	.01	.00	0	1.55	.24	0.0	.
males																		
JS	27.6	41.2	12.8	9.9	1.2	4.2	1.3	1.8	15.9	0.6	1.9	.06	.01	.01	5.50	.70	16.5	.08
PrB	12.7	28.4	27.9	6.3	5.6	2.7	2.9	1.8	15.4	1.0	0.5	.33	.03	.03	.	.	17.3	.06
CP	40.6	48.0	15.9	8.9	2.6	3.5	1.3	0.2	7.3	1.6	0.8	.01	.00	0	6.80	.12	1.9	.04
PrA	10.3	38.4	16.7	10.7	8.1	9.9	0.7	0.0	10.3	3.4	0.2	.15	.00	0	1.35	.20	31.1	.01
CB	32.9	36.3	30.0	5.4	4.4	6.1	1.3	1.2	8.4	1.1	2.1	.05	.02	0	1.90	.90	0.0	.07

Appendix 3.2a: Percent time males and females of two pairs of oystercatchers spent in behaviours during Stage IIa; Egg Laying.

Pair	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	OT	INC	INC'	COP
females																			
FC	16.5	19.4	44.1	6.4	5.1	7.9	0.8	0.1	4.1	0.7	3.2	0.00	0.29	0.00	3.7	2.6	5.7	0.4	0.0
JS	17.6	22.4	18.4	32.7	4.4	1.2	1.8	2.7	10.4	0.2	0.0	0.00	0.02	0.01	2.0	5.0	1.1	6.6	0.1
males																			
FC	10.2	12.2	42.3	13.9	0.9	1.8	0.1	1.6	8.0	0.7	1.3	0.01	0.50	0.02	4.2	3.1	12.6	0.5	0.0
JS	3.2	8.4	19.1	10.9	0.0	0.0	3.1	6.8	15.5	0.3	0.1	0.40	0.14	0.05	2.1	4.8	36.3	0.2	0.1

Appendix 3.2: Percent time males and females of six pairs of oystercatchers spent in behaviours during Stage II; Incubation (day 2-13).

	Behaviour																	
Pair	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	INC	OT	COP
females																		
PrB	6.8	9.7	5.8	0.3	0.0	0.0	1.1	0.6	2.1	0.3	0.2	0.07	0.00	0.01	2.7	76.3	0.00	0.00
FC	23.1	25.3	11.1	2.9	0.0	0.0	0.9	0.9	2.1	0.7	1.4	0.01	0.57	0.01	0.0	52.9	0.00	0.00
JS	21.2	25.8	7.0	1.0	0.4	2.7	2.2	0.8	6.9	0.4	0.2	0.06	0.00	0.02	1.8	50.5	0.00	0.00
CB	27.8	35.3	12.1	4.7	0.0	0.3	0.7	0.4	9.9	0.4	0.6	0.01	0.09	0.00	0.4	28.1	0.44	0.02
N31	4.8	9.8	7.3	0.0	0.0	0.0	0.6	2.3	5.1	0.2	0.1	0.00	0.00	0.00	0.0	74.5	0.84	0.00
AI	.	.	4.3	5.3	0.1	0.0	.	.	3.9	0.4	.	0.00	0.13	0.00	0.2	63.5	.	0.00
males																		
PrB	6.4	9.7	33.0	21.3	0.0	0.0	3.6	0.4	7.4	1.3	0.2	0.23	0.34	0.10	3.3	12.3	0.79	0.00
FC	17.1	21.7	17.1	17.9	0.0	0.0	0.4	4.4	3.0	1.0	1.4	0.01	0.14	0.03	1.0	33.8	0.00	0.00
JS	23.8	26.3	12.1	4.8	0.0	0.0	1.4	1.7	9.3	0.7	0.4	0.11	0.02	0.16	1.1	41.8	0.00	0.00
CB	11.7	20.6	11.2	2.6	0.1	0.0	0.7	0.9	2.7	0.4	1.8	0.00	0.11	0.01	0.0	54.8	0.83	0.02
N31	28.7	35.2	11.5	9.7	5.0	6.6	4.0	0.4	10.3	0.3	1.2	0.01	0.00	0.01	0.3	14.8	2.54	0.00
AI	.	.	13.7	8.1	0.0	0.0	.	.	5.4	0.7	.	0.00	0.82	0.00	0.3	33.9	.	0.00

Appendix 3.3: Percent time males and females of six pairs of oystercatchers spent in behaviours during Stage III; Incubation (day 14-hatching).

	Behaviour																
Pair	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	INC	OT
females																	
CB	18.7	28.6	5.5	3.6	0.1	0.0	1.5	0.4	7.2	0.3	0.3	0.00	0.01	0.02	0.1	47.4	1.7
FC	30.4	32.5	7.8	4.6	0.1	0.0	1.4	1.1	6.0	0.4	0.5	0.00	0.19	0.01	0.1	44.9	0.0
JS	8.6	31.3	5.3	1.2	1.3	1.8	1.0	0.1	4.1	0.4	0.4	0.14	0.05	0.08	0.3	52.5	19.9
PrB	4.3	17.9	14.8	1.9	0.0	0.0	0.5	0.1	1.9	0.3	0.0	0.01	0.14	0.01	0.3	58.3	9.6
N31	15.0	26.0	4.2	0.0	0.0	0.0	0.9	1.0	9.2	0.4	0.1	0.01	0.00	0.05	0.2	57.9	12.0
AI	.	.	7.4	2.2	0.0	0.0	.	.	6.3	0.4	.	.	0.01	0.02	0.0	47.3	.
males																	
CB	17.7	30.2	12.4	0.9	0.1	0.0	2.0	0.7	7.5	0.5	1.9	0.10	0.03	0.06	0.0	42.6	0.0
FC	19.4	21.8	9.9	6.4	0.0	0.0	1.5	0.7	5.1	0.6	1.4	0.06	0.08	0.19	0.3	51.2	0.0
JS	14.2	18.7	8.9	8.1	0.4	1.3	2.3	1.0	9.4	1.7	0.5	0.37	0.07	0.12	0.4	44.3	6.7
PrB	10.8	18.8	18.7	14.1	0.0	0.3	2.4	1.2	7.5	1.2	0.1	0.12	0.12	0.04	0.4	32.6	6.9
N31	17.8	37.8	15.4	5.4	0.0	0.0	1.5	0.3	7.8	0.4	2.1	0.02	0.06	0.01	0.6	37.9	0.0
AI	.	.	7.9	1.1	0.1	0.0	.	.	3.4	0.9	.	.	0.06	0.11	0.0	46.9	.

Appendix 3.4a: Percent time males and females of two pairs of oystercatchers spent in behaviours during Stage IVa; Hatching.

	Behaviour															
Pair	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	BRO
females																
JS	14.1	23.5	6.8	0.1	0.0	0.0	1.1	0.3	3.2	0.3	0.4	0.00	0.12	0.0	1.0	61.6
N31	16.0	28.7	2.7	0.0	0.0	0.0	3.0	0.1	14.3	0.2	0.0	0.02	0.11	0.0	15.1	53.8
males																
JS	26.7	33.5	14.7	3.8	0.0	0.0	1.4	0.7	7.4	0.1	0.4	0.06	0.22	0.0	0.9	36.8
N31	9.9	20.9	12.3	6.7	0.6	1.0	2.5	0.1	10.6	0.2	0.4	0.01	0.32	0.0	0.0	43.8

Appendix 3.4: Percent time males and females of four pairs of oystercatchers spent in behaviours during Stage IV; Chick rearing (day 2-10).

Pair	Behaviour																	
	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	BRO	FC	FFC
females																		
JS	10.2	15.3	14.0	3.7	2.0	3.5	2.7	0.3	2.1	0.5	0.1	0.00	0.00	0.26	0.0	51.5	1.5	2.3
CB	10.6	12.4	23.9	10.2	0.0	3.2	1.1	1.1	5.1	0.3	0.4	0.03	0.31	0.07	0.0	36.8	1.9	4.8
N41	12.0	17.3	17.5	3.3	4.3	7.5	5.7	0.0	7.4	0.8	0.4	0.00	2.69	0.21	0.0	13.6	5.1	9.7
AI	.	.	12.1	18.3	0.4	2.4	.	.	7.7	0.1	.	.	3.91	0.23	.	25.3	1.8	.
males																		
JS	16.3	23.8	21.0	9.5	4.5	4.4	2.3	1.7	7.2	0.6	0.4	0.01	0.00	0.35	0.0	6.6	5.2	8.7
CB	5.6	13.5	24.3	22.4	1.6	5.1	1.2	2.1	5.0	0.3	2.1	0.11	0.22	0.11	0.0	13.2	1.8	5.7
N41	19.6	27.1	11.5	11.0	2.7	6.5	5.1	0.4	10.3	1.0	0.8	0.02	2.59	0.20	0.0	3.5	7.2	9.5
AI	.	.	17.8	22.2	0.9	4.4	.	.	8.6	0.2	.	.	1.96	0.22	.	15.4	3.3	.

Appendix 3.5: Percent time males and females of seven pairs of oystercatchers spent in behaviours during Stage V; Chick Rearing (day 11-30).

	Behaviour																	
Pair	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	BRO	FC	FFC
females																		
GR	.	.	14.8	18.9	1.7	14.1	4.3	.	3.5	0.2	.	0.08	3.3	0.07	.	0.0	5.2	.
PB	.	.	18.8	21.6	0.1	0.7	3.5	.	7.5	0.4	0.1	0.00	4.7	0.04	.	14.6	1.9	.
N22	21.1	21.2	14.0	24.1	0.6	4.1	1.8	2.0	7.1	0.6	0.2	0.00	0.8	0.00	0.0	9.4	7.2	6.9
AI	.	.	7.1	15.5	6.2	21.2	1.8	.	4.2	1.6	0.9	0.01	0.2	0.00	0.0	3.7	4.9	3.2
N55	22.1	22.1	34.4	22.8	4.0	2.1	2.7	0.5	3.0	0.3	0.0	0.00	0.0	0.00	0.0	0.0	3.4	4.7
N41	14.3	14.3	10.9	12.1	5.5	23.8	3.3	0.1	10.2	0.5	0.4	0.05	0.3	0.16	0.0	0.0	3.2	12.2
JS	13.5	17.1	14.1	15.1	2.7	4.8	2.8	1.0	5.8	0.6	0.8	0.03	0.3	0.08	1.5	9.3	11.0	14.4
males																		
GR	.	.	21.9	25.7	0.3	1.3	3.4	.	7.9	0.3	.	0.04	0.6	0.05	.	0.0	2.6	.
PB	.	.	24.6	23.5	0.5	4.5	3.4	.	4.0	0.4	2.8	0.01	0.7	0.08	0.1	3.0	0.5	.
N22	15.7	17.5	26.8	32.1	0.1	6.5	2.5	0.7	8.4	0.7	2.1	0.02	1.0	0.03	2.2	0.0	1.5	1.8
AI	.	.	7.5	22.5	1.5	12.9	2.4	.	3.9	2.0	2.0	0.04	0.0	0.00	.	0.0	5.8	2.7
N55	30.9	30.9	21.8	16.2	0.6	7.8	3.3	0.2	10.3	0.3	0.0	0.00	0.0	0.00	0.0	0.0	2.5	5.9
N41	12.6	12.6	7.6	17.9	0.5	12.6	4.7	0.1	20.2	0.5	0.8	0.03	0.1	0.07	0.0	0.0	2.4	11.3
JS	16.3	22.0	14.0	16.5	2.2	8.6	3.5	0.9	8.1	0.4	2.0	0.16	0.0	0.09	0.0	5.4	10.9	9.4

Appendix 3.6: Percent time males and females of six pairs of oystercatchers spent in behaviours during Stage VI; Chick Rearing (> 30 days).

	Behaviour																
Pair	FO	adjFO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	FC	FFC
females																	
N22	18.9	23.2	12.5	19.3	0.8	9.2	4.3	0.9	12.1	0.3	0.2	0.02	0.30	0.0	3.6	6.0	6.6
N41	24.9	35.0	4.9	15.1	1.1	21.2	2.2	0.1	9.2	0.1	0.0	0.00	0.30	0.2	0.0	1.5	1.8
N55	6.7	6.7	26.1	38.6	0.0	0.0	3.7	0.6	7.5	0.2	0.0	0.00	0.00	0.0	0.0	4.9	11.2
JS	21.1	25.9	11.4	23.5	2.0	4.2	1.4	0.1	11.6	0.3	0.2	0.01	0.01	0.0	4.0	7.9	6.0
AI	.	.	8.3	13.0	1.6	22.3	.	.	10.9	0.7	0.1	0.03	0.10	0.0	.	.	.
GR	.	.	11.3	28.7	1.3	12.0	.	.	10.5	.	.	.	1.40	0.0	.	3.7	.
males																	
N22	22.2	27.9	19.1	18.1	1.7	5.8	2.5	0.3	12.4	0.7	0.1	0.08	0.48	0.0	6.4	1.6	4.0
N41	24.5	34.8	8.4	23.2	0.1	9.0	4.2	0.4	11.6	0.1	0.0	0.00	0.40	0.0	0.9	2.8	3.0
N55	17.4	20.1	12.5	25.2	0.5	15.5	4.1	0.3	9.9	0.2	0.4	0.00	0.00	0.0	0.0	4.7	6.5
JS	19.9	30.3	8.9	20.5	0.8	4.8	2.1	0.1	11.6	0.3	1.0	0.02	0.01	0.0	9.4	6.6	5.6
AI	.	.	5.2	14.8	1.4	17.8	.	.	9.7	0.8	0.5	0.05	0.05	0.0	0.0	.	.
GR	.	.	19.4	23.2	1.2	4.9	.	.	12.3	.	.	.	1.79	0.0	.	0.6	.

Appendix 4.1: Frequency of occurrence / 700 min of behaviours by males and females of five pairs of oystercatchers during Stage I; Prenesting.

Pair	FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	NP	OT	COP
females																	
JS	33.7	83.2	16.0	5.2	5.2	12.0	1.5	33.7	20.5	7.6	0.0	0.2	0.5	16.2	5.0	3.3	6.7
PrB	23.7	115.1	15.3	13.2	3.5	30.0	9.8	37.6	36.3	2.7	0.6	2.0	0.7	.	.	1.8	6.9
CP	36.6	75.4	17.0	6.8	6.5	12.4	6.8	19.6	37.7	3.9	0.0	0.0	0.0	8.8	2.3	0.5	3.6
PrA	24.4	112.3	22.7	22.7	11.7	5.2	1.7	52.9	51.8	1.2	0.0	0.0	0.0	4.6	1.2	3.6	1.2
CB	42.1	87.9	0.9	9.4	7.0	4.2	5.1	18.7	29.9	11.3	1.4	0.0	0.5	9.8	8.9	0.0	3.7
males																	
JS	30.1	94.6	11.8	3.6	2.6	18.0	3.1	27.0	19.6	8.1	2.3	0.5	3.0	27.0	12.3	3.3	6.7
PrB	23.2	140.8	15.2	11.6	1.4	38.5	15.2	49.3	34.8	3.3	7.9	0.7	4.3	.	.	6.9	6.9
CP	33.8	96.3	15.4	5.1	2.0	16.4	8.5	22.9	30.1	3.8	0.7	0.3	0.6	27.0	5.7	0.5	3.6
PrA	27.7	131.1	18.0	23.4	13.8	3.0	1.2	36.7	43.9	2.3	9.6	0.0	0.0	14.4	8.0	4.4	1.2
CB	31.4	118.6	11.9	8.4	6.2	10.6	12.8	20.4	24.8	13.8	1.7	0.4	4.4	11.5	10.9	0.0	3.7

Appendix 4.2: Frequency of occurrence / 700 min of behaviours by males and females of six pairs of oystercatchers during Stage II; Incubation (day 2-13).

Pair	FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	INC	OT	COP
females																	
PrB	11.6	25.5	0.8	0.0	0.0	15.3	9.1	7.6	14.4	2.8	1.1	0.0	0.7	9.2	8.8	0.0	0.0
FC	24.2	103.3	6.3	0.0	0.0	8.1	30.6	7.0	21.1	18.8	0.7	3.9	0.7	0.0	9.4	0.0	0.0
JS	23.6	46.2	3.1	2.7	1.8	34.9	17.0	13.8	11.5	3.5	2.6	0.0	1.3	0 .0	8.0	0.4	0.0
CB	22.6	53.9	7.8	0.4	0.4	11.5	18.8	15.9	7.1	4.6	0.8	0.4	0.0	0.0	3.8	0.0	0.8
N31	6.3	33.0	0.0	0.0	0.0	13.4	22.3	11.0	8.5	2.5	0.0	0.0	0.0	0.0	5.1	0.8	0.0
AI	.	22.8	6.8	0.8	0.0	.	.	12.1	7.6	.	0.0	1.5	0.0	1.5	4.5	.	0.0
males																	
PrB	14.8	113.6	35.5	0.4	0.0	46.6	24.2	31.1	28.3	3.2	11.1	4.7	5.1	1.7	7.6	0.8	0.0
FC	23.4	101.8	9.4	0.0	0.0	8.4	37.0	13.3	20.4	21.1	1.5	1.5	1.5	4.7	10.2	0.0	0.0
JS	24.8	59.5	4.9	0.0	0.0	29.3	19.7	13.8	13.8	4.9	3.1	1.3	2.6	5.6	7.1	0.0	0.0
CB	8.5	43.1	3.0	0.4	0.0	14.6	16.5	7.4	5.9	7.5	0.0	1.3	1.3	0.0	4.2	0.8	0.8
N31	21.8	73.7	12.7	10.2	5.1	33.2	18.0	24.5	10.2	11.0	1.6	0.0	0.8	0.0	3.4	2.5	0.0
AI	.	54.6	14.4	0.0	0.0	.	.	20.5	15.9	.	0 0	0.7	0.0	1.5	3.8	.	0.0

Appendix 4.2a: Frequency of occurrence / 700 min of behaviours by males and females of two pairs of oystercatchers during Stage IIa; Egg Laying.

Pair	Behaviour FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	OT	INC'	INC	COP
females																		
FC	14.1	125.8	15.6	17.1	12.6	8.1	8.1	19.3	27.5	8.9	0.0	5.2	0.0	9.7	2.2	10.4	5.5	2.7
JS	11.8	69.8	23.6	2.1	1.1	26.8	6.4	23.6	5.4	1.1	0.0	1.1	1.1	7.5	1.1	9.1	5.1	4.0
males																		
FC	13.2	203.3	37.5	2.9	0.7	2.2	18.4	52.3	26.5	13.9	1.5	10.3	2.9	18.4	2.2	16.7	5.6	2.8
JS	5.3	66.2	13.8	0.0	0.0	38.5	16.0	39.5	9.6	2.1	1.1	2.1	6.4	11.7	1.1	15.2	7.1	4.0

Appendix 4.3: Frequency of occurrence of behaviours / 700 min by males and females of six pairs of oystercatchers during Stage III; Incubation (day 13-hatching).

Pair	Behaviour															
	FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	BT	INC	OT
females																
CB	19.9	52.3	4.4	0.4	0.0	21.0	18.6	12.7	9.9	4.0	0.7	0.3	1.9	1.2	7.1	0.4
FC	18.9	46.6	4.3	0.8	0.0	16.3	17.1	15.9	12.4	7.4	0.0	2.3	0.3	0.8	5.0	0.0
JS	8.2	26.3	1.6	1.2	0.4	18.9	7.0	11.9	8.2	7.0	0.8	0.8	0.8	2.1	4.1	1.6
PrB	4.2	25.9	2.4	0.0	0.0	9.1	4.8	5.2	11.1	0.8	1.1	1.1	0.3	2.3	5.4	2.7
N31	7.1	30.7	0.0	0.0	0.0	16.6	9.6	15.8	12.3	5.3	1.7	0.8	0.0	2.6	6.2	2.3
AI	.	30.6	3.6	0.0	0.0	.	.	11.5	4.8	.	.	1.1	1.5	0.4	4.4	.
males																
CB	26.9	70.9	1.2	0.4	0.0	26.9	26.9	16.6	15.5	14.3	5.1	0.3	1.9	0.4	6.3	0.0
FC	21.0	59.0	7.0	0.0	0.0	18.6	25.6	15.9	10.5	8.9	1.9	1.1	5.8	2.3	5.4	0.0
JS	12.5	49.6	7.4	1.6	1.2	30.8	17.2	19.7	14.8	7.4	6.1	1.6	3.2	2.1	4.9	1.2
PrB	12.8	86.9	18.2	0.0	0.4	3.9	24.0	31.0	26.4	2.7	4.6	2.3	2.7	3.9	4.6	1.9
N31	12.3	50.2	7.7	0.0	0.0	19.3	13.9	11.6	12.1	10.8	1.5	0.7	0.7	2.3	6.2	0.0
AI	.	25.8	2.0	0.4	0.0	.	.	7.1	6.3	.	.	0.8	0.8	0.0	4.8	.

Appendix 4.4: Frequency of occurrence of behaviours / 700 min by males and females of four pairs of oystercatchers during Stage IV; Chick Rearing (day 2-10).

Pair	FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	BRO	FC	FFC
females																	
JS	11.8	96.1	11.9	2.4	0.8	27.8	47.2	7.9	15.9	1.6	0.0	0.7	6.3	0.0	7.1	16.7	.
CB	19.2	104.2	13.1	0.0	2.3	24.8	44.1	11.6	10.1	6.2	1.5	3.0	3.8	0.0	7.0	13.1	12.6
N41	19.4	81.3	8.6	17.2	12.4	62.2	42.1	22.0	22.6	6.7	0.0	17.2	12.4	0.0	2.9	41.5	37.7
AI	.	90.3	41.5	4.9	5.7	.	.	33.4	5.2	.	.	39.8	5.6	.	7.3	14.6	.
males																	
JS	11.5	139.0	23.8	7.1	4.0	56.1	84.1	32.6	14.3	4.0	1.5	0.0	12.7	0.0	3.2	36.5	.
CB	26.3	124.7	30.2	3.9	4.6	17.8	43.4	17.8	12.4	10.1	1.5	2.3	4.6	0.0	6.2	17.8	30.7
N41	28.0	72.5	19.8	10.3	12.9	60.0	37.8	30.2	22.0	7.8	2.5	14.6	8.6	0.0	0.9	43.2	28.0
AI	.	120.4	49.4	4.9	2.4	.	.	39.0	11.4	.	.	16.2	8.1	.	4.9	15.4	.

Appendix 4.4a: Frequency of occurrence / 700 min of behaviours by males and females of two pairs of oystercatchers during Stage IVa; Hatching.

Pair	Behaviour														
	FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	BRO
females															
JS	18.1	50.5	0.8	0.0	0.0	21.7	24.1	10.4	2.5	5.6	0.8	0.8	2.4	0.8	1.8
N31	5.4	20.5	0.0	0.6	0.0	17.0	3.5	15.8	7.3	0.0	0.7	0.7	3.3	2.6	7.2
males															
JS	28.5	85.4	10.9	0.0	0.0	42.3	25.0	14.1	2.5	5.5	0.8	0.8	3.9	0.0	12.9
N31	4.5	23.8	10.6	1.9	2.6	18.1	7.5	20.5	6.6	2.6	1.3	1.9	1.9	0.0	14.5

Appendix 4.5: Frequency of occurrence of behaviours / 700 min by males and females of seven pairs of oystercatchers during Stage V; Chick Rearing (day 11-30).

	Behaviour																
Pair	FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	BRO	FC	FFC
females																	
GR	.	82.1	32.8	19.5	20.3	46.9	.	23.4	8.6	3.1	0.7	11.7	3.9	.	0.0	31.3	.
PB	.	104.8	45.1	1.8	1.3	41.6	.	32.7	17.7	1.3	0.0	27.8	3.5	.	3.2	19.9	.
N22	26.7	93.5	54.3	6.7	5.0	17.5	92.6	30.0	30.0	4.2	0.0	6.6	0.0	0.0	1.6	50.9	27.5
AI	.	57.9	25.8	25.3	22.8	26.6	.	22.4	30.8	3.8	1.2	2.9	0.8	.	3.5	57.0	.
N55	15.6	141.8	66.2	7.2	4.1	29.0	24.8	11.4	10.3	10.3	0.0	0.0	0.0	.	0.0	29.0	18.9
N41	21.6	51.4	20.1	19.3	23.3	40.1	9.6	30.5	14.4	0.8	1.6	4.8	9.6	0.0	0.0	33.7	25.9
JS	27.4	85.0	22.5	5.0	5.0	31.8	38.5	16.7	18.6	8.0	1.0	3.9	3.9	0.3	7.9	122.5	50.0
males																	
GR	.	123.5	57.1	5.5	4.7	50.0	.	43.8	11.7	5.5	0.7	5.4	3.9	.	0.0	19.5	.
PB	.	102.6	51.3	4.0	3.5	36.3	.	26.5	19.9	4.0	3.9	7.0	3.9	.	1.6	14.1	.
N22	14.5	125.3	69.0	0.8	4.3	9.4	40.9	31.5	35.8	14.5	0.8	6.8	2.5	0.8	9.4	17.9	9.4
AI	.	74.3	49.0	8.4	12.7	23.2	.	19.8	38.8	8.4	3.8	0.0	0.0	.	0.0	32.1	.
N55	11.9	107.3	51.0	8.3	11.4	27.1	23.9	39.6	8.3	0.0	0.0	0.0	0.0	0.0	0.0	14.4	13.1
N41	23.7	55.3	28.9	1.6	12.8	56.9	16.0	38.5	16.8	3.2	1.6	4.0	8.8	0.0	0.0	29.2	28.3
JS	24.3	81.1	23.3	5.6	7.2	45.2	41.5	18.5	17.9	10.7	2.4	0.2	4.5	0.0	2.4	77.3	40.8

Appendix 4.6: Frequency of occurrence of behaviours / 700 min by males and females of six pairs of oystercatchers during Stage VI; Chick Rearing (> 30 days).

	Behaviour															
Pair	FO	STBU	STBOB	SIBU	SIBOB	WA	FL	PR	GP	AP	PA	HUG	HUA	OT	FC	FFC
females																
N22	33.4	64.5	31.0	7.3	9.2	47.0	46.5	34.4	13.6	6.3	1.0	7.3	1.4	1.4	60.0	36.6
N55	29.9	134.3	66.7	0.0	0.0	65.6	95.5	28.9	11.6	0.0	0.0	0.0	0.0	0.0	55.0	40.5
N41	44.8	42.2	20.7	3.9	11.9	30.3	5.2	28.6	5.6	0.0	0.0	5.6	15.1	0.0	31.3	15.6
JS	28.1	47.9	21.5	6.3	4.6	19.8	8.3	18.3	10.3	1.9	1.7	0.6	0.4	1.0	74.9	31.8
AI	22.0	43.2	17.0	21.1	20.1	40.0	.	28.2	18.0	1.4	2.7	2.4	3.1	.	40.0	23.7
GR	.	81.2	49.4	15.0	14.0	38.1	.	36.3	3.2	0.5	0.5	19.0	1.4	.	1.4	.
males																
N22	39.4	81.4	37.6	6.7	6.7	36.0	23.8	35.7	21.4	7.6	0.9	8.1	5.2	2.8	53.7	30.4
N55	22.3	122.7	59.6	10.7	13.3	76.5	73.6	51.6	5.3	5.3	0.0	0.0	0.0	0.0	43.5	32.9
N41	45.9	41.4	31.8	1.6	6.4	41.1	16.3	35.0	7.2	0.0	0.0	2.4	3.2	0.8	42.1	21.0
JS	29.9	41.1	17.7	2.7	3.2	30.9	10.3	19.0	11.0	3.6	0.8	0.4	0.2	1.5	49.1	28.2
AI	23.2	45.9	23.5	7.5	13.6	37.3	.	23.8	21.1	3.1	3.4	0.7	0.3	.	60.0	29.2
GR	.	93.4	50.8	6.8	6.3	46.2	.	44.0	7.2	4.1	0.0	17.2	2.3	.	12.7	.

Appendix 5.1: Summary statistics of bout durations of behaviours by females and males of five pairs of oystercatchers during Stage I; Prenesting.

Pair		Behaviour												
		FO	OT	STBU	STBOB	SIBU	SIBOB	PR	GP	PA	HUG	HUA	BT	AP
females														
JS	n	135	16	333	64	21	21	135	76	0	1	2	65	31
	$\bar{x}$	6.2	34.1	1.2	5.4	1.3	13.1	4.2	0.2	.	.03	0.1	2.2	1.7
	s	7.7	39.8	1.6	5.1	1.9	9.9	4.9	0.2	.	.	.	1.6	4.2
	median	3.4	15.8	0.7	3.7	0.5	10.4	2.2	0.1	.	.03	0.1	1.8	0.5
PrB	n	34	4	165	22	19	5	54	48	1	3	1	-	5
	$\bar{x}$	5.1	57.0	2.1	6.1	3.8	3.7	3.3	0.3	1.4	0.6	0.6	.	0.6
	s	5.9	61.6	2.7	6.8	5.6	3.2	4.0	0.3	.	0.5	.	.	1.2
	median	2.6	36.8	1.1	4.1	1.7	2.9	2.1	0.1	1.4	0.5	0.1	.	0.1
CP	n	112	2	231	52	21	20	60	88	0	0	0	27	13
	$\bar{x}$	9.6	20.3	1.2	5.6	2.7	8.2	2.8	0.4	.	.	.	1.2	1.4
	s	9.6	.	2.2	6.4	3.1	6.8	2.4	0.2	.	.	.	1.2	2.5
	median	6.3	20.3	0.6	3.4	2.3	7.5	2.1	0.2	.	.	.	0.9	0.3
PrA	n	42	9	193	39	39	20	91	73	0	0	0	8	2
	$\bar{x}$	3.4	59.4	1.4	3.6	4.5	7.6	3.0	0.4	.	.	.	1.0	0.1
	s	3.4	34.2	2.0	3.1	6.7	8.4	3.5	0.3	.	.	.	0.8	.
	median	2.2	60.5	0.7	2.5	1.1	3.9	2.0	0.2	.	.	.	0.7	0.1
CB	n	90	0	188	2	20	15	40	56	3	0	1	21	27
	$\bar{x}$	8.4	.	1.7	2.4	5.0	8.4	2.4	0.3	0.1	.	.03	1.2	0.1
	s	7.5	.	2.7	.	7.6	9.2	2.4	0.2	.01	.	.	0.8	1.9
	median	6.1	.	0.9	2.4	1.8	4.4	2.0	0.2	0.1	.	.03	0.8	0.3
males														
JS	n	117	16	367	46	14	10	105	82	9	2	12	105	33
	$\bar{x}$	6.1	35.2	1.2	7.3	2.9	14.2	5.0	0.3	0.2	0.2	0.1	1.8	2.0
	s	5.4	39.1	1.7	6.8	4.7	11.9	6.0	0.1	0.4	.	0.1	1.5	3.4
	median	3.7	17.9	0.7	5.7	0.7	10.9	2.8	0.2	0.1	0.2	0.1	1.5	0.6
PrB	n	32	6	194	21	16	2	68	52	11	1	6	-	6
	$\bar{x}$	3.8	43.9	1.8	3.8	4.5	17.2	2.7	0.2	0.2	0.4	0.6	.	1.0
	s	4.5	51.9	2.5	6.5	4.1	.	3.3	0.1	0.1	.	0.8	.	1.8
	median	1.9	24.9	0.9	1.6	3.5	17.2	1.5	0.1	0.1	0.4	0.2	.	0.1
CP	n	99	2	282	45	15	6	67	140	2	1	2	79	14
	$\bar{x}$	8.4	25.2	1.4	4.9	4.3	14.4	2.7	0.4	0.1	0.1	0.4	2.1	1.4
	s	8.4	.	2.9	4.7	5.5	19.9	2.7	0.3	.	.	.	1.9	2.5
	median	4.8	25.2	0.6	4.2	0.9	5.7	1.8	0.1	0.1	0.1	0.4	1.5	0.2
PrA	n	46	11	218	30	39	23	66	65	89	0	0	24	4
	$\bar{x}$	2.6	49.5	1.3	4.7	3.6	7.4	2.5	0.5	0.4	.	.	1.0	0.7
	s	3.1	37.5	1.7	3.9	6.5	7.3	3.1	0.9	0.8	.	.	0.6	1.1
	median	1.4	53.6	0.7	3.7	1.1	5.6	1.2	0.3	0.2	.	.	0.9	0.3
CB	n	71	0	268	27	19	14	46	64	4	1	10	26	3
	$\bar{x}$	7.3	.	1.9	3.3	3.9	7.2	2.9	0.3	0.2	0.4	0.2	1.2	1.1
	s	7.5	.	2.6	2.9	8.1	7.7	2.4	0.2	0.3	.	0.3	0.6	1.7
	median	5.1	.	0.9	2.7	0.8	5.0	2.3	0.2	0.1	0.4	0.1	1.0	0.3

Appendix 5.2: Summary statistics of bout durations of behaviours by females and males of six pairs of oystercatchers during Stage II: Incubation (day 2-13).

Pair		Behaviour FO	OT	STBU	STBOB	SIBU	SIBOB	PR	GP	PA	HUG	HUA	BT	INC	AP
females															
JS	n	50	1	104	7	6	4	31	26	6	0	3	15	18	8
	$\bar{x}$	6.3	50.5	1.1	2.2	1.0	10.7	3.4	0.3	0.2	.	0.1	1.9	43.1	0.4
	s	6.9	.	1.8	1.4	1.7	6.3	2.8	0.2	0.2	.	0.1	1.1	27.7	0.3
	median	3.1	50.5	0.5	1.9	0.2	13.4	2.6	0.2	0.1	.	0.0	2.1	43.9	0.3
PrB	n	28	0	64	1	0	0	19	36	3	0	2	23	22	6
	$\bar{x}$	4.1	.	1.6	2.2	.	.	1.8	0.2	0.3	.	0.1	2.0	60.5	0.7
	s	4.9	.	1.9	.	.	.	2.0	0.1	0.4	.	.	3.2	59.1	1.1
	median	1.9	.	0.8	2.2	.	.	0.6	0.1	0.1	0.0	0.1	1.4	45.2	0.4
CB	n	47	0	125	18	1	1	37	17	2	1	0	2	9	11
	$\bar{x}$	8.6	.	1.6	4.3	0.7	4.6	4.1	0.5	0.1	1.5	.	3.1	35.4	0.9
	s	12.0	.	1.9	3.4	.	.	4.4	0.4	0.1	.	.	.	22.9	1.2
	median	5.4	.	0.9	3.7	0.7	4.5	3.1	0.3	0.1	1.5	.	3.1	36.0	0.6
FC	n	30	0	132	8	0	0	9	27	1	5	1	0	12	24
	$\bar{x}$	6.7	.	0.8	3.3	.	.	2.0	0.3	0.1	1.0	0.5	.	37.2	0.5
	s	5.7	.	0.9	3.1	.	.	2.2	0.2	.	0.9	.	.	49.2	0.4
	median	4.9	.	0.4	2.2	.	.	0.8	0.2	0.1	0.6	0.5	.	21.4	0.4
N31	n	7	1	39	0	0	0	13	10	0	0	0	1	6	3
	$\bar{x}$	5.4	5.9	1.5	.	.	.	3.2	0.2	.	.	.	0.2	102.6	0.4
	s	2.7	.	7.8	.	.	.	7.1	0.1	.	.	.	.	64.7	0.2
	median	4.8	5.9	0.2	.	.	.	0.5	0.2	.	.	.	0.2	98.8	0.4
AI	n	-	-	30	9	1	0	16	10	0	2	0	2	6	3
	$\bar{x}$	.	.	1.3	5.4	1.1	.	2.3	0.4	.	0.6	.	0.7	87.2	0.3
	s	.	.	1.3	7.1	.	.	2.4	0.2	.	.	.	.	43.7	0.1
	median	.	.	0.7	3.8	1.1	.	1.0	0.5	.	0.6	.	0.7	109.5	0.3
males															
JS	n	54	0	134	11	0	0	31	31	7	3	6	12	16	11
	$\bar{x}$	6.7	.	1.4	6.8	.	.	4.7	0.4	0.2	0.1	0.4	1.5	36.1	0.6
	s	5.3	.	2.5	5.6	.	.	3.9	0.5	0.3	0.1	0.7	1.1	21.3	0.5
	median	5.3	.	0.5	6.3	.	.	3.8	0.1	0.1	0.1	0.1	1.5	33.3	0.6
PrB	n	33	2	285	89	1	0	78	71	28	12	13	32	19	8
	$\bar{x}$	3.0	19.9	2.0	4.2	0.2	.	1.5	0.3	0.1	0.5	0.1	1.8	10.2	0.5
	s	2.7	.	3.2	4.2	.	.	1.8	0.7	0.1	0.4	0.1	1.4	15.1	0.7
	median	2.1	19.9	1.0	3.3	0.2	.	0.8	0.2	0.1	0.3	0.1	1.3	2.6	0.2
CB	n	18	2	99	7	1	0	17	14	0	3	3	0	10	15
	$\bar{x}$	9.6	21.9	1.8	6.0	2.3	.	2.3	0.5	.	0.6	0.5	.	41.2	1.9
	s	8.4	.	3.3	5.6	.	.	1.8	0.5	.	0.5	0.6	.	23.6	3.6
	median	8.2	21.9	0.7	4.1	2.3	.	2.5	0.3	.	0.6	0.9	.	44.9	0.7
FC	n	29	0	130	12	0	0	17	26	2	2	2	6	13	27
	$\bar{x}$	4.9	.	1.2	11.1	.	.	1.6	0.4	0.1	0.6	0.2	1.4	19.6	0.5
	s	4.4	.	2.0	8.8	.	.	1.4	0.5	.	.	.	1.1	10.9	0.3
	median	3.4	.	0.6	8.0	.	.	0.9	0.2	0.1	0.6	0.2	1.3	19.6	0.4
N31	n	23	3	89	15	12	6	29	12	2	0	1	1	4	13
	$\bar{x}$	9.2	5.7	1.0	5.3	3.4	9.0	2.9	0.2	0.1	.	.03	2.9	26.5	0.8
	s	8.7	4.2	1.3	5.2	5.2	11.9	2.9	0.1	.	.	.	.	8.2	0.5
	median	6.3	7.6	0.5	4.2	1.2	4.3	1.7	0.2	0.1	.	.03	2.8	26.6	0.6
AI	n	-	-	72	19	0	0	27	21	0	1	0	2	5	6
	$\bar{x}$	.	.	1.8	3.9	.	.	1.8	0.3	.	0.8	.	1.2	54.7	0.9
	s	.	.	3.3	5.3	.	.	1.9	0.3	.	.	.	.	12.2	0.5
	median	.	.	0.6	2.8	.	.	1.2	0.2	.	0.8	.	1.2	53.0	0.9

Appendix 5.3: Summary statistics of bout durations of behaviours by females and males of six pairs of oystercatchers during Stage III; Incubation (day 14-hatch).

Pair		Behaviour FO	OT	STBU	STBOB	SIBU	SIBOB	PR	GP	PA	HUG	HUA	BT	INC	AP
females															
JS	n	15	4	64	4	3	1	27	20	2	2	2	5	10	17
	$\bar{x}$	7.4	69.8	1.4	4.9	7.2	31.3	2.6	0.4	1.2	0.5	0.8	0.9	67.1	0.4
	s	12.5	26.2	3.1	3.5	6.8	.	3.4	0.3	.	.	.	0.9	29.5	0.3
	median	2.7	79.5	0.5	4.8	7.8	31.3	1.8	0.3	1.2	0.5	0.8	0.7	66.6	0.3
PrB	n	9	7	65	6	0	0	13	27	2	3	1	6	14	2
	$\bar{x}$	7.2	24.7	4.0	5.7	.	.	2.5	0.3	0.1	0.8	0.1	0.9	79.6	0.1
	s	3.5	13.3	13.5	6.1	.	.	2.9	0.2	.	0.3	.	0.6	38.8	0.1
	median	6.6	31.3	0.8	4.2	.	.	0.2	0.1	0.1	0.9	0.1	0.7	82.7	0.1
CB	n	44	1	132	11	1	0	29	25	2	1	5	3	18	10
	$\bar{x}$	6.6	30.7	1.1	5.8	2.4	.	4.2	0.3	.03	0.3	0.1	0.6	46.3	0.1
	s	6.9	.	1.5	5.7	.	.	4.1	0.2	.	.	0.1	0.4	32.3	0.3
	median	4.6	30.7	0.6	3.8	2.4	.	3.8	0.2	.03	0.3	0.1	0.5	47.7	0.6
FC	n	48	0	120	11	2	0	38	32	0	6	1	2	13	19
	$\bar{x}$	11.0	.	1.2	7.5	1.0	.	2.7	0.3	.	0.6	0.1	1.1	43.9	0.5
	s	13.1	.	1.9	9.4	.	.	3.1	0.2	.	0.5	.	.	28.4	0.4
	median	7.1	.	0.5	3.5	0.9	.	1.5	0.2	.	0.4	0.1	1.1	38.8	0.4
N31	n	8	3	35	0	0	0	18	16	1	1	0	3	8	6
	$\bar{x}$	14.8	23.4	1.1	.	.	.	4.6	0.2	0.1	0.5	.	0.6	65.6	0.2
	s	10.4	13.3	1.6	.	.	.	6.0	0.1	.	.	.	0.4	43.2	0.1
	median	10.2	19.7	0.5	.	.	.	1.3	0.2	0.1	0.5	.	0.6	67.8	0.1
AI	n	-	-	71	9	0	0	29	12	-	3	4	4	11	-
	$\bar{x}$	.	.	1.6	4.3	.	.	3.8	0.6	.	0.1	0.1	0.1	69.6	.
	s	.	.	2.1	4.1	.	.	4.5	0.9	.	0.1	0.1	0.1	39.9	.
	median	.	.	0.7	3.3	.	.	2.4	0.2	.	0.1	0.1	0.1	57.9	.
males															
JS	n	28	3	121	18	4	3	46	36	15	4	8	5	12	18
	$\bar{x}$	8.0	25.1	1.3	7.3	1.6	7.5	3.5	0.8	0.4	0.3	0.3	1.3	55.6	0.5
	s	11.8	22.4	1.9	10.8	2.8	6.5	4.2	2.3	0.6	0.3	0.4	1.6	38.4	0.3
	median	4.1	29.5	0.6	3.8	0.2	6.9	1.9	0.3	0.2	0.2	0.1	0.8	45.1	0.4
PrB	n	30	5	224	47	0	1	80	64	11	6	7	10	12	7
	$\bar{x}$	5.9	25.1	1.5	5.4	.	5.9	1.7	0.4	0.2	0.4	0.1	0.8	44.2	0.3
	s	6.9	21.3	3.4	5.7	.	.	2.1	0.5	0.1	0.3	0.1	0.7	22.5	0.4
	median	2.8	15.6	0.6	3.7	.	5.9	0.8	0.2	0.2	0.3	0.1	0.7	38.4	0.1
CB	n	57	0	179	3	1	0	37	39	13	1	5	1	16	36
	$\bar{x}$	4.6	.	1.2	5.2	1.3	.	3.4	0.3	0.1	0.6	0.2	0.2	41.3	0.9
	s	4.4	.	1.5	1.9	.	.	3.9	0.3	0.3	.	0.2	.	24.8	1.5
	median	2.8	.	0.7	5.0	1.3	.	1.8	0.1	0.1	0.6	0.2	0.2	37.7	0.6
FC	n	52	0	152	18	0	0	36	27	3	3	15	6	14	23
	$\bar{x}$	6.5	.	1.2	6.4	.	.	2.2	0.4	0.4	0.5	0.2	0.8	58.5	1.1
	s	6.4	.	1.5	5.7	.	.	2.1	0.7	0.5	0.3	0.3	0.5	29.5	1.5
	median	3.8	.	0.6	5.1	.	.	1.6	0.2	0.1	0.6	0.1	0.8	60.5	0.7
N31	n	14	0	65	10	0	0	15	16	2	1	1	3	8	14
	$\bar{x}$	10.1	.	2.1	4.9	.	.	4.7	0.3	0.1	0.6	0.1	1.9	38.3	1.4
	s	10.4	.	2.9	4.4	.	.	3.9	0.3	.	.	.	2.3	26.6	2.2
	median	7.1	.	1.0	4.1	.	.	3.2	0.1	0.1	0.6	0.1	0.8	30.8	0.7
AI	n	-	-	65	5	1	0	18	16	-	2	2	0	12	-
	$\bar{x}$	.	.	2.1	3.8	1.1	.	3.4	0.9	.	0.6	1.0	.	62.1	.
	s	.	.	6.5	1.5	.	.	3.5	2.5	.	.	.	.	41.4	.
	median	.	.	0.7	3.1	1.1	.	1.9	0.2	.	0.6	1.1	.	53.8	.

Appendix 5.4: Summary statistics of bout durations of behaviours by females and males of four pairs of oystercatchers during Stage IV; Chick rearing (day 2-10).

Pair		Behaviour FO	OT	STBU	STBOB	SIBU	SIBOB	PR	GP	PA	HUG	HUA	AP	BRO	FFC	FC
females																
JS	n	14	0	120	14	3	1	10	20	0	1	8	2	9	15	21
	$\bar{x}$	6.0	.	1.0	2.3	6.0	30.6	1.9	0.2	.	.01	0.3	0.5	50.4	1.4	0.6
	s	5.3	.	1.6	2.2	9.9	.	2.2	0.3	.	.	0.2	.	59.0	1.3	0.5
	median	3.4	.	0.4	1.5	0.3	30.6	1.1	0.1	.	.01	0.3	0.5	30.6	0.9	0.4
CB	n	21	0	135	17	0	3	15	13	2	4	5	8	9	-	17
	$\bar{x}$	5.7	.	1.6	5.4	.	9.7	3.0	0.2	0.2	0.7	0.1	0.4	35.5	.	1.0
	s	4.4	.	2.2	5.2	.	8.0	6.5	0.2	.	0.8	0.1	0.2	24.5	.	1.3
	median	4.0	.	0.8	3.6	.	10.3	1.5	0.1	0.2	0.4	0.1	0.4	28.9	.	0.5
N41	n	19	0	85	9	18	13	20	27	0	18	13	7	3	37	49
	$\bar{x}$	4.3	.	1.5	2.7	1.7	4.3	2.6	0.3	.	1.1	0.1	0.4	36.9	1.9	0.8
	s	3.9	.	2.1	2.8	3.5	4.5	3.5	0.2	.	1.2	0.1	0.7	35.6	1.2	0.6
	median	3.0	.	0.8	1.3	0.7	1.7	1.3	0.2	.	0.8	0.1	0.1	22.9	1.2	0.6
AI	n	-	-	111	51	6	7	41	7	0	49	7	-	9	-	18
	$\bar{x}$	.	.	0.9	3.1	0.6	2.9	1.6	0.1	.	0.7	0.3	.	22.6	.	0.9
	s	.	.	1.3	3.5	0.5	2.8	1.8	.03	.	0.7	0.3	.	14.7	.	0.8
	median	.	.	0.5	1.9	0.3	1.1	0.6	0.1	.	0.5	0.3	.	19.7	.	0.6
males																
JS	n	29	0	172	30	9	5	30	18	2	0	16	5	4	35	45
	$\bar{x}$	3.9	.	1.1	2.8	4.4	13.8	2.1	0.3	0.1	.	0.2	0.6	14.4	2.2	1.0
	s	3.9	.	1.6	2.7	8.8	10.1	2.3	0.5	.	.	0.3	0.3	10.5	3.1	1.1
	median	3.2	.	0.5	1.8	0.7	18.3	1.3	0.1	0.1	.	0.1	0.6	12.7	1.3	0.5
CB	n	13	0	161	39	5	6	22	16	2	3	6	13	8	-	23
	$\bar{x}$	4.5	.	1.4	5.2	2.9	7.7	2.0	0.2	0.5	0.7	0.2	0.5	15.6	.	0.7
	s	4.2	.	2.1	5.1	3.7	4.5	2.4	0.1	.	0.8	0.1	0.4	14.5	.	0.6
	median	2.5	.	0.5	3.2	1.7	6.2	1.2	0.1	0.5	0.4	0.1	0.5	10.6	.	0.5
N41	n	29	0	84	23	12	15	32	27	3	17	10	7	1	29	5
	$\bar{x}$	4.9	.	1.1	3.9	1.8	3.5	2.5	0.3	0.1	1.2	0.2	0.4	28.7	2.4	1.0
	s	5.1	.	1.7	3.8	3.3	3.5	2.1	0.3	.04	1.7	0.2	0.6	.	3.1	0.8
	median	3.1	.	0.6	3.0	0.4	1.9	2.1	0.2	0.1	0.8	0.1	0.6	28.7	1.1	0.8
AI	n	-	-	148	61	6	3	48	14	0	20	10	-	6	-	19
	$\bar{x}$	.	.	1.0	3.1	1.3	12.7	1.5	0.1	.	0.8	0.2	.	23.2	.	1.5
	s	.	.	1.8	4.2	1.1	7.9	1.4	0.1	.	1.3	0.2	.	18.2	.	1.4
	median	.	.	0.5	1.8	1.3	15.0	1.0	0.1	.	0.7	0.1	.	15.7	.	1.2

Appendix 5.5: Summary statistics of bout durations of behaviours by females and males of seven pairs of oystercatchers during Stage V; Chick rearing (day 11-30).

		Behaviour														
Pair		FO	OT	STBU	STBOB	SIBU	SIBOB	PR	GP	PA	HUG	HUA	AP	BRO	FFC	FC
females																
JS	n	99	1	320	85	19	19	61	69	4	5	15	30	10	181	443
	$\bar{x}$	3.4	40.2	1.1	4.6	3.6	6.5	2.5	0.3	0.2	1.7	0.1	0.7	24.6	2.0	0.6
	s	3.4	.	2.3	4.4	5.5	2.6	2.6	0.3	0.3	3.1	0.2	0.5	15.6	3.1	0.8
	median	2.3	40.2	0.5	2.9	1.6	6.3	1.6	0.1	0.1	.03	0.1	0.6	24.2	1.1	0.4
N22	n	32	0	112	65	8	6	36	36	0	8	0	5	2	33	61
	$\bar{x}$	5.5	.	1.0	3.1	0.6	5.8	1.6	0.2	.	0.9	.	0.3	39.4	1.8	1.0
	s	3.6	.	1.5	3.6	0.4	13.1	2.6	0.1	.	1.1	.	0.1	.	0.9	1.5
	median	4.6	.	0.5	2.0	0.5	0.5	0.8	0.1	.	0.5	.	0.3	39.4	1.5	0.5
N41	n	25	0	64	25	24	29	36	18	2	6	12	1	0	30	39
	$\bar{x}$	3.8	.	1.5	4.2	2.0	7.2	2.4	0.3	0.2	0.5	0.1	0.3	.	3.3	0.7
	s	3.9	.	1.8	4.3	3.2	8.1	2.7	0.2	.	0.4	.03	.	.	2.8	1.1
	median	2.8	.	0.8	3.2	0.5	5.0	1.3	0.1	0.2	0.4	0.1	0.3	.	2.5	0.4
N55	n	14	0	137	64	7	4	11	10	0	0	0	1	0	17	28
	$\bar{x}$	7.3	.	1.7	2.4	3.8	3.6	1.8	0.2	.	.	.	.01	.	1.7	0.8
	s	5.3	.	2.7	2.4	4.1	1.7	2.5	0.2	.	.	.	.	.	0.8	0.6
	median	5.1	.	0.6	1.6	2.6	3.6	0.8	0.1	.	.	.	.01	.	1.7	0.8
AI	n	-	0	137	61	60	54	53	73	2	7	2	9	4	34	135
	$\bar{x}$	.	.	0.8	4.2	1.7	6.5	1.3	0.4	0.1	0.5	.04	1.6	15.5	1.5	0.6
	s	.	.	1.1	4.8	2.9	7.4	1.2	0.8	.	0.4	.	0.9	9.9	1.5	1.4
	median	.	.	0.5	2.5	0.5	4.2	0.9	0.2	0.1	0.3	.04	1.5	17.7	1.1	0.3
PB	n	-	-	237	102	4	3	74	40	0	63	8	3	4	-	45
	$\bar{x}$	.	.	1.3	3.3	0.4	3.5	1.6	0.1	.	1.2	0.1	0.7	25.1	.	0.7
	s	.	.	1.6	3.8	0.1	5.5	1.7	0.1	.	1.4	.03	0.7	19.1	.	0.3
	median	.	.	0.6	2.0	0.4	0.5	1.1	0.1	.	0.5	0.1	0.3	26.8	.	0.6
GR	n	-	-	105	42	25	26	30	11	0	15	5	-	0	-	40
	$\bar{x}$	.	.	1.3	4.0	0.6	4.8	1.0	0.2	.	2.0	0.1	.	.	.	1.2
	s	.	.	1.8	3.6	1.2	4.7	0.9			3.9	0.1	.	.	.	0.7
	median	.	.	0.5	3.2	0.3	4.0	0.6	0.1	.	0.4	0.2	.	.	.	1.2
males																
JS	n	84	0	303	87	21	27	65	67	8	1	17	40	3	141	267
	$\bar{x}$	4.7	.	1.2	4.9	2.8	8.3	3.2	0.2	0.4	.03	0.1	1.3	16.0	1.6	1.0
	s	6.1	.	2.1	5.2	3.6	12.8	3.3	0.1	0.4	.	0.1	1.7	12.6	1.9	1.2
	median	2.5	.	0.6	2.9	0.8	4.0	1.6	0.1	0.3	.03	0.1	0.8	20.3	0.9	0.6
N22	n	17	1	147	81	1	5	36	41	1	8	3	17	0	11	21
	$\bar{x}$	7.6	18.5	1.5	3.3	0.7	10.7	1.8	0.1	0.2	0.7	0.1	1.0	.	1.3	0.6
	s	7.4	.	2.0	3.0	.	11.9	2.4	0.1	.	1.1	0.1	1.4	.	0.7	0.6
	median	3.9	18.5	0.7	2.2	0.7	4.1	0.9	0.1	0.2	0.3	0.1	0.6	.	1.2	0.4
N41	n	26	0	69	36	2	16	44	21	2	5	11	4	0	31	32
	$\bar{x}$	3.7	.	1.0	4.3	2.1	6.9	3.9	0.3	0.1	0.3	0.1	0.4	.	2.8	0.6
	s	2.9	.	1.1	5.3	.	5.6	3.8	0.2	.	0.2	.03	0.5	.	3.5	0.5
	median	2.7	.	0.6	2.5	2.1	3.9	2.8	0.2	0.1	0.2	0.1	0.2	.	1.4	0.4
N55	n	10	0	103	49	8	11	36	8	0	0	0	0	0	11	14
	$\bar{x}$	12.4	.	1.4	2.2	0.5	4.8	1.9	0.8	.	.	.	.	.	3.6	1.2
	s	8.9	.	2.3	2.6	0.6	6.2	2.0	0.2	.	.	.	.	.	2.7	0.9
	median	9.1	.	0.7	0.9	0.2	2.4	1.2	0.2	.	.	.	.	.	3.0	0.8
AI	n	-	-	176	116	20	30	47	92	6	0	0	20	0	20	76
	$\bar{x}$	.	.	0.7	3.2	1.3	7.1	1.4	0.5	0.1	.	.	1.6	.	2.2	1.3
	s	.	.	0.9	3.0	2.1	9.5	1.8	0.3	.02	.	.	2.4	.	2.5	2.1
	median	.	.	0.4	2.3	0.4	4.3	0.7	0.2	0.1	.	.	1.2	.	1.4	0.7
PB	n	-	-	232	116	9	8	60	45	1	16	16	9	2	-	32
	$\bar{x}$	.	.	1.7	3.2	0.9	8.9	1.0	0.1	0.1	0.7	0.1	4.9	10.2	.	0.3
	s	.	.	2.7	3.5	1.1	11.7	1.1	0.1	.	0.8	0.2	11.6	.	.	0.2
	median	.	.	0.7	1.9	0.4	3.8	0.6	0.1	0.1	0.4	0.1	0.9	10.2	.	0.2
GR	n	-	-	158	73	7	6	56	15	0	1	7	-	0	-	25
	$\bar{x}$	.	.	1.2	3.1	0.3	1.9	1.3	0.2	.	0.4	0.8	.	.	.	0.9
	s	.	.	2.0	3.8	0.2	0.7	1.3	0.2	.	.	1.1	.	.	.	1.4
	median	.	.	0.8	2.1	0.3	0.7	0.8	0.2	.	0.4	0.5	.	.	.	0.3

Appendix 5.6: Summary statistics of bout durations of behaviours by females and males of six pairs of oystercatchers during Stage VI; Chick rearing (> day 30).

Pair		Behaviour													
		F O	O T	S T B U	S T B O B	S I B U	S I B O B	P R	G P	P A	H U G	H U A	A P	F F C	F C
N22	n	61	3	133	64	15	19	71	28	13	2	15	3	67	108
	x	3.9	17.7	1.4	4.3	0.8	6.9	2.4	0.2	0.2	0.2	0.3	0.1	1.3	0.7
	s	3.7	6.6	1.8	4.5	1.2	7.8	2.4	0.1	0.4	0.2	0.3	0.1	1.1	1.2
	median	2.8	20.2	0.7	2.8	0.2	4.5	1.5	0.1	0.2	0.2	0.1	0.1	1.1	0.2
N41	n	43	0	53	26	5	15	36	7	0	0	7	19	15	30
	x	3.9	.	0.8	5.1	1.9	12.4	2.2	0.1	.	.	0.4	0.1	0.9	0.4
	s	3.6	.	0.8	7.8	3.7	15.2	2.6	0.1	.	.	0.2	0.1	0.7	0.4
	median	2.7	.	0.6	1.7	0.3	6.1	1.6	0.1	.	.	0.3	0.1	0.7	0.2
N55	n	19	0	116	59	0	0	32	13	4	0	0	0	42	57
	x	2.6	.	1.6	4.8	.	.	2.2	0.2	0.5	.	.	.	2.2	0.9
	s	2.2	.	2.9	8.2	.	.	2.3	0.2	0.1	.	.	.	1.5	0.7
	median	2.1	.	0.6	2.2	.	.	1.1	0.1	0.5	.	.	.	1.5	0.6
JS	n	115	5	227	102	30	22	87	50	9	8	3	2	130	306
	x	5.2	26.4	1.7	7.6	2.2	6.3	4.3	0.2	0.9	0.1	0.2	.03	1.4	0.8
	s	5.4	12.5	2.9	10.8	2.9	3.9	4.9	0.2	0.5	0.1	0.1	.	1.7	1.1
	median	3.0	34.3	0.6	4.0	1.1	6.6	2.4	0.2	0.9	.04	0.2	.03	0.8	0.3
AI	n	50	1	127	50	62	59	83	53	4	7	7	9	54	91
	x	3.6	35.1	1.3	5.2	1.3	7.5	2.6	0.3	0.8	.03	0.4	0.1	1.6	0.6
	s	3.0	.	1.9	5.2	2.0	7.3	3.2	0.3	0.7	.02	0.2	0.1	1.8	0.9
	median	3.2	35.1	0.7	4.1	0.4	5.1	1.6	0.2	0.7	.03	0.5	0.1	1.0	0.3
GR	n	-	-	179	109	33	30	80	9	-	0	42	3	-	44
	x	.	.	0.9	4.1	0.6	6.2	1.9	0.1	.	.	0.5	0.1	.	1.3
	s	.	.	1.5	4.6	1.0	8.5	2.4	.04	.	.	0.6	.01	.	0.8
	median	.	.	0.5	2.4	0.3	3.6	0.9	0.1	.	.	0.5	0.1	.	0.2
males															
N22	n	72	6	171	79	14	14	75	45	16	2	17	11	55	97
	x	3.9	15.6	1.6	3.4	1.8	6.1	2.3	0.1	0.1	0.6	0.4	0.1	1.0	0.2
	s	4.6	15.4	2.7	3.4	2.9	6.0	2.3	0.1	0.1	0.7	0.3	0.1	1.0	0.4
	median	2.2	9.7	0.5	2.4	0.1	4.3	1.8	0.1	0.1	0.6	0.3	0.1	0.5	0.1
N41	n	48	1	52	40	2	8	44	9	0	0	3	4	2	44
	x	3.7	8.2	1.4	5.1	0.6	9.8	2.3	0.2	.	.	0.6	0.1	1.1	0.5
	s	3.7	.	2.4	7.9	.	10.6	2.9	0.1	.	.	0.2	.01	0.8	0.7
	median	2.7	8.2	0.6	1.8	0.6	7.7	1.2	0.1	.	.	0.7	0.6	0.9	0.2
N55	n	21	0	105	59	12	15	48	8	6	0	0	0	34	45
	x	5.9	.	0.9	3.2	0.3	7.9	1.5	0.2	0.5	.	.	.	2.2	1.1
	s	5.1	.	1.7	3.4	0.3	8.7	1.7	0.2	.03	.	.	.	1.9	0.8
	median	4.6	.	0.4	2.1	0.2	4.0	1.1	0.1	0.0	.	.	.	1.3	0.8
JS	n	110	7	195	84	13	15	90	52	17	4	2	1	104	181
	x	4.7	45.0	1.4	8.0	1.9	10.5	4.1	0.2	1.9	0.2	0.2	0.1	1.8	1.1
	s	5.7	26.8	2.2	9.7	2.3	8.2	4.6	0.1	2.8	0.3	.	.	2.1	1.4
	median	2.4	49.7	0.7	6.7	0.8	8.3	2.2	0.2	0.1	0.2	0.2	0.1	1.2	0.5
AI	n	43	0	135	69	22	40	70	62	9	10	2	1	54	11
	x	2.7	.	0.7	4.1	1.2	8.6	2.6	0.3	1.1	0.1	0.4	0.1	1.3	0.7
	s	2.4	.	0.9	5.6	2.2	9.4	2.9	0.3	1.5	0.1	.	.	1.4	1.1
	median	2.0	.	0.4	2.1	0.3	6.4	1.6	0.2	0.0	0.4	0.4	0.1	1.1	0.3
GR	n	-	-	206	112	15	14	97	20	-	0	38	5	-	28
	x	.	.	1.4	3.2	1.2	5.4	1.9	0.1	.	.	0.7	0.1	.	0.3
	s	.	.	3.7	3.8	1.6	5.2	2.1	0.1	.	.	0.9	.02	.	0.3
	median	.	.	0.5	2.2	0.5	3.6	1.1	0.1	.	.	0.5	0.1	.	0.3

VITA

Surname: Purdy

Given Names: Margaret Anita

Place of Birth: Amherst, Nova Scotia

Date of Birth: January 8, 1955

Educational Institutions Attended, with Dates of Entering and Leaving:

Acadia University	1972	to	1976
University of Victoria	1981	to	1985

Degrees, Diplomas, Etc., Awarded, with Dates and Names of Institutions:

BSc (Honours)	1976	Acadia University

Honours and Awards:

University of Victoria Fellowship	1982/1983
University of Victoria Scholarship	1983/1984

Publications:

Purdy, M. A. 1985. Mirrored windows for use in blinds. J. of Field Ornithol. 56:68-69.

Gaston, A. J., D. G. Noble, M. A. Purdy. 1983. Monitoring breeding biology parameters for murres Uria spp.: Levels of accuracy and sources of bias. J. of Field Ornithol. 54:275-282.

PARTIAL COPYRIGHT LICENSE

Title of Thesis

Parental behaviour and role differentiation in the

Black Oystercatcher (*Haematopus bachmani*).

Author [redacted]
Signature [redacted]

Margaret A. Purdy
Name

November 22, 1985
Date