Reproductive Strategies in the Oystercatchers (Aves: Haematopodidae)

by

Erica Nol

Department of Zoology
University of Toronto

A Thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy in the
University of Toronto

c Erica Nol 1984

ABSTRACT

Reproductive strategies of the American Oystercatcher (*Haematopus palliatus*), which lays a modal clutch of three eggs in Virginia and two eggs in Argentina, were compared with the Blackish Oystercatcher (*H. ater*), which lays a modal clutch of two eggs. Average egg size of *H. palliatus* in Virginia was correlated with the size of the laying female. Egg-size ordering occurred within clutches, the first-laid egg being smaller than the second egg and about equal in volume to the third. The second egg is largest possibly because it has the highest probability of hatching, and the resulting sibling hierarchy aids in the efficient distribution of food. Obligatory parental care results in highly complementary sex roles. Sex roles are indistinguishable during pre-laying. During laying, males chase conspecifics more than females. Females incubate more but use less energy to incubate than males. Males forage more to provision young and take longer trips, but wait longer between each trip than females. Energetic expenditure by each sex is approximately equal.

In Argentina, mean clutch size of *H. ater* was 1.91 eggs. Mean clutch size of the sympatric *H. p. durnfordi* was 2.31 eggs. The climate, the birds' behaviour, and their habitats were more predictable in Argentina than in Virginia. Of the three taxa, *H. p. palliatus* fed the least during pre-laying but the most during chick-rearing. *H.*

ater and H. p. durnfordi fed equally in pre-laying and probably equally during chick-rearing. Less food availability for the chicks may account for lower average clutch size of H. palliatus in Argentina. Differences in maximum clutch size of H. ater and H. palliatus in Argentina probably results from past selective pressures that parallelled the speciation events. H. ater and other melanistic oystercatchers are non-migratory, have rocky nest-sites and rocky inter-tidal feeding areas, lay modal 2-egg clutches, and have limited colonizing abilities. A combination of environmental predictability, nest-site availability and density-dependent mortality probably accounts for lower maximum clutch size in these oystercatchers. The more adaptable colonizing forms, H. ostralegus and H. palliatus, are usually migratory, sometimes lay four eggs, nest on unstable substrates, and feed on variable and less predictable food resources.

RESUME

Les strategies reproductives de l'Huitrier américain (Haematopus palliatus), qui pond une couvée modale de trois oeufs en Virginie et de deux oeufs à l'Argentine, étaient comparéss avec celles de l'Huitrier noirâtre (H. ater), qui pond une couvée modale de deux oeufs. La grandeur moyenne des oeufs de H. palliatus à la Virginie corréspondait avec la grandeur de la femelle pondante. En dedans les couvées, la grandeur des oeufs consecutifs présentait un ordre, le premier pondu étant plus petit que le deuxième et à peu près du même volume que le troisième. La probabilité de l'eclosion du deuxième oeuf est probablement plus élevé en consequence de sa grandeur supérieure, et la hiérarchie des confrères qui s'en résulte aide à achever une distribution efficace de la nourriture. Quoique les rôles sexuels sont indistincts pendant l'avant-ponte, la nécessité du soin parental exige des rôles sexuels font complémentaires. Durant la ponte, les mâles poursuivent des conspécifiques plus que les femelles. Le femelles couvent pour une plus longue durée, mais elles utilisent moins d'énergiue que des mâles. Les mâles fourragent au provisions plus que des femelles et leurs fourrages sont de plus longue durée, mais ils attendent entre les excursions consecutives pour plus longtemps que des femelles.

A l'Argentine, la grandeur moyenne de couvée chez H. ater était 1,91 oeufs; celle de sympatrique H. p. durnfordi était 2,31 oeufs. Le climat, le comportement des oiseaux, et leurs habitats étaient plus prédirable en Argentine que dans la Virginie. De ces trois taxa, H. p. palliatus se nourrissait le moindre durant l'avant-ponte, mais plus quand avec l'enfants. H. ater et H. p. durnfordi se nourrissaient

équitablement en tous les étages. La prédictabilité et les vers budgets d'énergie annuelle qui s'en résultaient peuvent expliquer la plus basse grandeur moyenne des couvées chez H. palliatus à l'Argentine. Les différences entre la grandeur maximum de couvée chez H. ater et H. palliatus en Argentine resultent probablement des pressions selectifs au temps passé qui allaient parrallèlement à des événements de speciation. H. ater et les autre huitriers mélanistiques sont non-migratoires, nichent à des sites rocheux, se nourrissent dans les zones rocailleuses de l'entre-marée, pondent les couvées moyenne de deux oeufs et démontrent la capacité limitée pour la colonisation. La combinaison de la prédictabilité d'environnement, la disponibilité des sites de nid et la mortalité correspondant à la densité expliquent probablement la plus basse grandeur maximum des couvées chez ces huitriers. Les formes colonisantes plus adaptables, H. ostralegus et H. palliatus, sont migratoires d'habitude, ponteut parfois quatres oeufs, nichent sur des substrats instable et se nourrissent aux ressources variantes et moins prédirables.

TABLE OF CONTENTS

Abstract i

Resume iii

Table of Contents v

Acknowledgements x

CHAPTER 1: GENERAL INTRODUCTION 1

CHAPTER 2: CLUTCH INITIATION DATES, CLUTCH SIZE AND EGG SIZE OF THE AMERICAN OYSTERCATCHER IN VIRGINIA 4

1.Introduction 4

2.Methods 6

2.1.Study area 6

2.2.Data collection 9

2.3.Statistical analysis 10

3.Results 12

3.1.Clutch initiation 12

3.2.Clutch size 17

3.3.Egg size 19

3.4.Female size 28

4.Discussion 29

CHAPTER 3: SEX ROLES IN THE AMERICAN OYSTERCATCHER 35

1.Introduction 35

2.Methods 38

2.1.Study area 38

2.2.Estimation of time budgets 39

2.3.Estimation of energy budgets 42

2.4.Statistical methods 44

3.Results 45

3.1.Sampling effort 45

3.2.Nesting and feeding areas 47

3.3.Time of day differences 48

3.4.Sex differences 48

3.5.Feeding trips 56

3.6.Anti-predator and territorial behaviour 60

3.6.1.Anti-predator behaviour - 'cooperative' model 60

3.6.2.Anti-predator behaviour - 'uncooperative' model .. 63

3.6.3.Territorial behaviour - 'cooperative' model 64

3.6.4.Territorial behaviour - 'uncooperative' model 64

3.7.Effect of stage of breeding 65

3.8.Multivariate descriptions 69

3.9.Sexual dimorphism 73

3.10.Energy expenditure over breeding cycle 76

4.Discussion 79

CHAPTER 4: LIFE-HISTORY TRAITS OF OYSTERCATCHERS AND ENVIRONMENTAL PREDICTABILITY 90

1.Introduction 90

2.Methods 93

2.1.Study animals 93

2.2.Daily time budgets 94

2.3.Feeding behaviour 95

2.4.Feeding path analysis 100

2.5.Egg parameters 103

2.6.Behavioural diversity 103

2.7.Habitat sampling 104

2.7.1.Habitats used by H. p. palliatus 104

2.7.2.Habitats used by H. p. durnfordi and H. ater 106

2.8.Territory quality and reproductive performance 107

2.9.Statistical analysis 108

2.10.Predictability of environment 110

3.Results 111

3.1.Clutch sizes 111

3.2.Lack's hypothesis (food limitation during chick-rearing) 111

3.2.1.Time budgets 111

3.2.2.Feeding efficiency 113

3.3.Food limitation during pre-laying 121

3.4.Environmental predictability hypothesis 123

3.4.1.Feeding behaviour 126

3.4.2.Variability in feeding behaviour 135

3.4.3.Analysis of feeding paths 136

3.4.4.Behavioural diversity 142

3.4.5.Variablity in egg parameters 155

3.4.6.Reproductive success 158

3.4.7.Habitat variability 158

3.4.8.Comparison of predictability across habitats in space and time 169

3.4.9.Climatic stability 172

4.Discussion 177

4.1.Food limitation hypotheses 173

4.2.Environmental predictability hypothesis 176

4.3.Life-history comparison of H. ater and H. p. durnfordi 179

SUMMARY 196

GLOSSARY 199

LITERATURE CITED 201

ACKNOWLEDGEMENTS

I wish to thank my supervisor, Dr. Allan J. Baker, for inspiring this study through his extensive familiarity with the oystercatchers of the world, and for convincing me that oystercatchers are indeed worthy of study. Dr. Baker has contributed extensively to my maturation as a scientist.

Others have contributed in less significant but important ways. Chris Robertson suggested the use of the International Instruments electronic event decoder. Wern Theil helped keep it operating. David Trueman was especially helpful in writing the programs to translate the event decoder output into usable forms. Particular thanks go to him for his extreme patience and willingness to assist. David Dunham provided an office space for long periods while I was transcribing tapes, and also provided various equipment. These loans are gratefully acknowleged here. Michael Gates wrote the program to analyse the digitized foraging data. Peter Fetterolf read and commented on the third chapter of the thesis. Members of my supervisory committee Drs. Jim Rising and David Dunham reviewed and commented on the thesis.

My field work in Virginia was made much more comfortable by the extreme hospitality of Cynthia and Edward Risley who allowed me to live in their beach house on Chincoteague. Barbara and Gary Howard provided friendship, meals and the

use of their boats. My field work was skillfully augmented by assistance from Steven Nash, Ann Rivers, Jan McDonnell, Tom Clark and Chris Risley. Access to Wallops island, Virgina was granted by the National Aeronautics and Space Administration officials at the Wallops Island facility. George Watson kindly allowed volumetric determinations of the eggs at the Smithsonian Institute and Ann Zimmerman loaned me her boat. Traps for removing raccoons from the study area were provided by Irvin Ailes of the Chincoteague National Wildlife Refuge.

The field work in Argentina was expedited by the efforts of Monica de Escardo of the Canadian Embassy in Buenos Aires, the Centro Nacional Patagonico in Puerto Madryn, and the Centro Turisma de Provincia del Chubut in Rawson. Alejandro Lynch, Mirtha Lewis, Ors Kovaks and Alberto Passera helped with the arrangements. Carol and Alberto Passera provided hospitality in Punta Tombo. The Department of Invertebrate Zoology of the Royal Ontario Museum identified the mollusk specimens from Argentina.

This study was supported by Natural Science and Engineering Research Council grants, a Pure and Applied Research Grant, and the Frank M. Chapman Memorial Fund.

This thesis is dedicated to my husband, Chris Risley, who assisted in the field in 1981, put up with long absences in other years, enthusiastically discussed various sections of the thesis, drew many of the figures, and generally made life easier throughout the period of this study.

Chapter 1: GENERAL INTRODUCTION

Because reproductive output is the only currency of natural selection, knowledge of how reproductive effort is apportioned through the lifetime of an individual, and how it is influenced by the environment is central to the understanding of evolution. Examples of semelparous animals or plants are nearly always associated with extremely unpredictable environments for the adults (Pianka 1970, Stearns 1976) Those animals and plants which live long lives and produce few young in each of many reproductive efforts live in stable environments for the adults, but usually highly unpredictable for the young (Pianka 1970). Between these two extremes lie the reproductive strategies of most species. If life-history patterns have evolved as adaptive responses to varying environments, then it should be shown that within a closely related group of organisms, selection in the form of local conditions can act to produce relatively longer-lived, slow-reproducing individuals, or short-lived fast-reproducing individuals.

Birds have annual fecundity patterns that are easy to measure (i.e. number of eggs laid), and therefore make good subjects for the study of life-history evolution. However, reproductive effort and clutch size are not synonymous because the latter does not measure cost, in terms of reproductive value (Williams 1966a, Cody 1971, Ricklefs 1974). If it is assumed that costs are proportional to the number of eggs laid, for birds with eggs of approximately equal size the cost factor can be

ignored. The important point here is that comparisons within taxa of equivalent rank will likely have fewer hidden values in the calculation of reproductive effort than comparisons among taxa.

Oystercatchers (Family: Haematopodidae, Sub-order: Charadrii) are like other shorebirds in laying only a small number of eggs (Maclean 1967). However the maximum clutch size laid by oystercatchers varies among species. The European Oystercatcher (Haematopus ostralegus), for example, lays as many as four eggs (Burton 1938, usually three), whereas the African Black Oystercatcher (H. moquini) rarely lays more than two eggs (Hockey 1983). The family has a cosmopolitan distribution (Baker 1973) but there do not seem to be any geographic correlates to the pattern of modal clutch size among species. In some places in the world species laying modal clutches of three and two eggs occur sympatrically (e. g. Australia, New Zealand, South America). These examples of sympatry provide excellent natural laboratories to examine the relationships between food, environmental predictability and fecundity.

This thesis presents the results of three major investigations. In Chapter 2, I document seasonal and annual patterns in clutch size, egg size and clutch initiation dates to elucidate the natural variability in these life-history traits within a single species of Haematopus. The objective of this chapter also is to gauge repeatability estimates of these characters for known females over several successive breeding seasons.

In Chapter 3, I attempt to measure components of reproductive effort not related to fecundity. I examine the time and energy costs of reproduction by male and female American Oystercatchers (Haematopus

palliatus) and discuss the relative contributions of each sex in relation to parental investment theory (Trivers 1972). Specifically I ask whether males and females apportion time or energy to reproduction differently on an annual basis. Oystercatchers have extensive parental care and the pattern of apportionment is discussed in relation to the specific requirements of rearing a brood.

In the final chapter I compare the predictability of the environment of the American Oystercatcher, with a maximum clutch size of four eggs, with that of the Blackish Oystercatcher (H. ater) with a maximum clutch size of two eggs. I assess predictability from a general perspective by using climatic stability as a measure of the degree to which oystercatchers live in uncertain environments. I then also examine habitat and behavioural predictability in detail. This is done to determine the extent to which the birds' lives reflect climatic stability and to investigate the causal relationship between clutch size and environmental predictability. The possibility that the proximate effects of food shortage limits clutch size in H. ater is examined. Finally, I look at patterns of life-history traits among the oystercatchers of the world to test the generality of the findings from this study.

Chapter 2: CLUTCH INITIATION DATES, CLUTCH SIZE AND EGG SIZE OF THE AMERICAN OYSTERCATCHER IN VIRGINIA

1. Introduction

Synchrony of clutch initiation dates, uniform egg size and four-egg clutches are assumed to be adaptations of many shorebirds (Charadrii and Scolopacii) for living within the constraints of high latitude breeding seasons. Clutch initiation dates occur over a very brief period (Holmes 1971) and replacement clutches are uncommon (Pitelka et al. 1974) because the period of abundant food resources is brief and the season is telescoped (Holmes 1972, Nettleship 1973, Pitelka et al. 1974). A definitive clutch of four eggs of similar size and shape apparently form the optimal configuration for minimizing the rate of heat loss when uncovered (Norton 1970).

Uniform egg size within a clutch also implies no differential allocation of parental care to the chicks (Miller 1979). Uniform chick size may be as important a consequence of four similarly-sized eggs as the energetic advantage during incubation, particularly since a definitive clutch of four is also found in many shorebirds nesting in the temperate zone (Maclean 1972) where heat conservation is less crucial.

Oystercatchers (Haematopodidae) are one of the few families of shorebirds whose young depend almost exclusively on the adults for food. Clutch size in this group is usually less than four eggs and this may be related to the extensive parental care (Maclean 1972). Egg size ordering within a clutch is undocumented in the oystercatchers but it might be expected to occur here rather than in shorebirds that do not feed their young. Through preferential feeding oystercatcher parents have greater potential for 'control' over which of their chicks survive (Alexander 1974). This potential control might be extended to the eggs, particularly if food is limiting, or variable (Howe 1976), preferential feeding impractical, and the probability of raising all chicks dependent on the food supply.

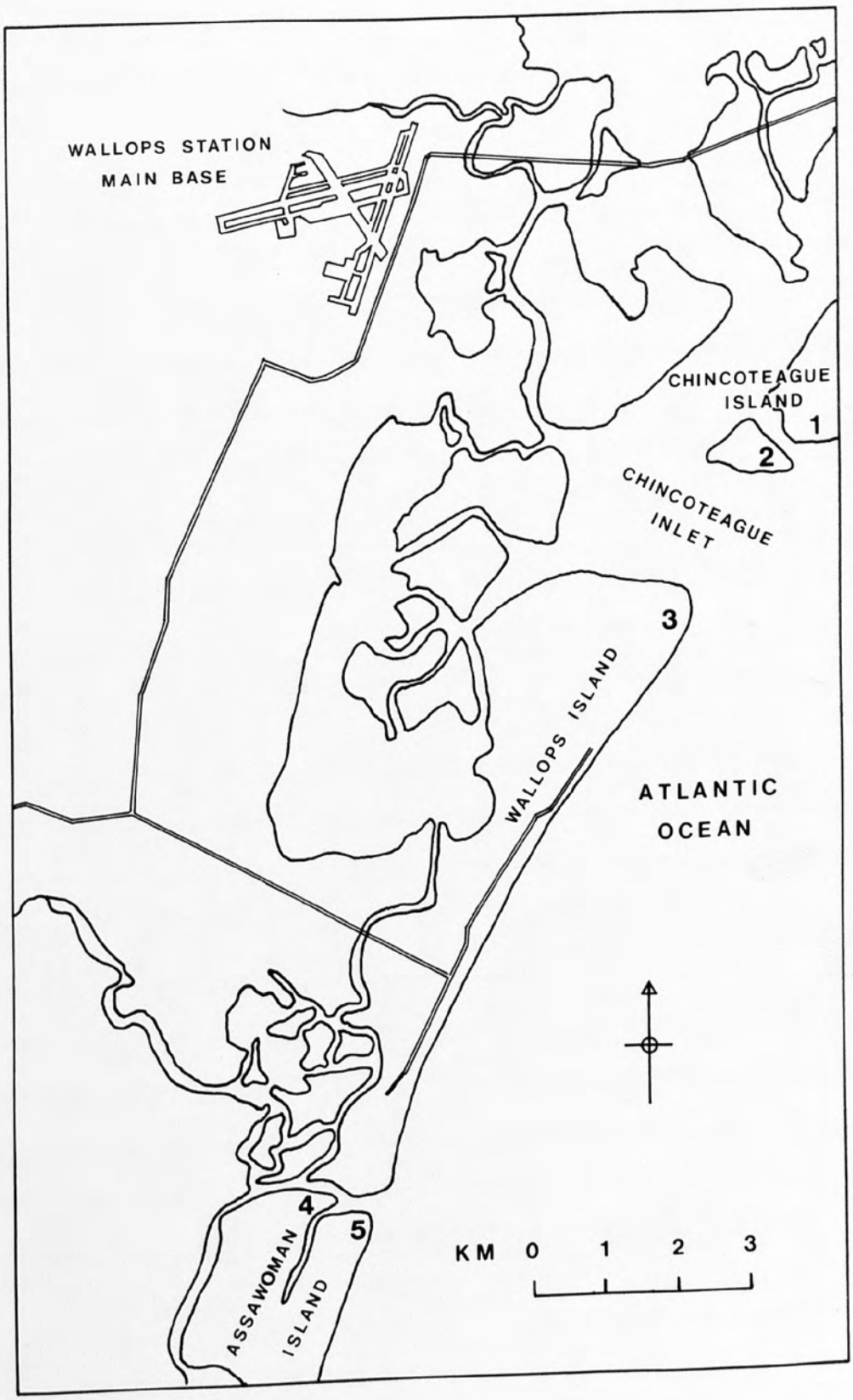
The purpose of this chapter is to document variations in clutch size and egg size in American Oystercatchers (Haematopus palliatus), and also to elucidate seasonal and annual patterns in the timing of egg laying. By comparing individual known females over several breeding seasons I have attempted to gauge repeatability measures (Falconer 1981) of the aforementioned characteristics as well as the effect of female size.

2. Methods

2.1. Study area

Study sites were located on Wallops and Assawoman islands, Virginia (37°50′N, 75°35′W) in 1978-1983, and also the salt marshes and dunes around the Chincoteague Channel, Virginia (37°55′N, 75°23′W) in 1981-1983. For purposes of comparing synchrony of clutch initiation dates among localities I divided the study area into five localities: 1) Chincoteague Island, 2) Chincoteague Point, 3) northern Wallops Island, 4) the sand spit of southern Wallops Island, and 5) Assawoman Island (Fig. 1). Field work was conducted at the study sites within the period 1 March to 31 July for six successive breeding seasons from 1978 to 1983. Observations in all seasons began by at least 6 April.

Fig. 1. Map of study area showing five breeding sites: (1) Chincoteague Island (mean of 5 nests per year), (2) Chincoteague Point ($\bar{x}$ = 13 nests), (3) northern Wallops Island ($\bar{x}$ = 7 nests), (4) the sand spit of southern Wallops Island ($\bar{x}$ = 8 nests), and (5) Assawoman Island ($\bar{x}$ = 6 nests).


WALLOPS STATION
MAIN BASE
CHINCOTEAGUE
ISLAND
1
2
CHINCOTEAGUE
INLET
3
WALLOPS ISLAND
ATLANTIC
OCEAN
4
5
ASSAWOMAN
ISLAND
KM 0 1 2 3

2.2. Data collection

Over the study period 60 adults (30 females, 30 males) were trapped at the nests using drop traps lined with fish net (Mills and Ryder 1979). The adults were banded with aluminum and unique colour band combinations, and also weighed and measured. From 1978-1980 all territories were searched periodically, although the clutch sequence (i.e., whether first or replacement clutch) or the order of egg laying were not always known. To obviate this problem, in the 1981-1983 breeding seasons I searched territories throughout the pre-laying and laying periods.

Eggs were marked, weighed and measured. All weights used in the analyses are of eggs weighed within 48 h of being laid. Weight can be difficult to determine in the field, particularly on windy days, whereas length and breadth measures are more precise. I therefore wanted a method for predicting volumes. Sixty-eight eggs from museum collections were filled with water to determine their volumes. Regression coefficients were calculated with volume as the dependent variable and the product egg length (EL) X breadth^2 (EB^2) as the independent variable (Väisänen 1969). The resultant formula was used to calculate volume for all eggs measured: Volume (cm^3) = 0.47736 X EL (mm) X EB^2 (mm^2) - 1.318 (mm^3) (R^2=0.96). Fresh egg weight (EW) was a good predictor of the calculated volume, as follows: Volume (cm^3) = 0.757 EW (g) + 5.96 (cm^3), R^2 = 0.87, n=170. In the subsequent text egg size and volume are used synonymously.

2.3. Statistical analysis.

The clearest method for detecting the effects of the female, clutch sequence and year on egg size is to look at the effects of each factor in two two-way designs (Sokal and Rohlf 1981). I tested for the effects using a mixed model two-way analysis of variance (ANOVA) with females as a random factor, and assumed no interaction between females and the fixed factor (e.g., year or clutch sequence). I then estimated the variation attributable to females and to the fixed factor and the significance levels of the two factors, using the interaction term as the error term. I used mean values to avoid the confounding effects of different cell sizes produced by different sized clutches. When using year as the main effect I examined only first clutches to avoid any confounding of clutch sequence in the design. In the comparison of means I used t-tests on every pair of means while controlling the experimentwise error rate by lowering the value of α to α/n where n is the number of paired comparisons made.

To test for differences in egg size across years, across clutches within a year, and in different-sized clutches I used one-way analysis of variance. I also tested for differences in egg size as a result of egg order with one-way analysis of variance.

The ratio of the between-individual component of variance to the total variance measures the correlation between repeated measurements of the same individual and is known as the repeatability of a character (Falconer 1981). Heritability, the resemblance between relatives, may be

much less than repeatability, but it cannot be greater (Falconer 1981). The within-individual component arises from environmental fluctuations between successive measures and the systematic effects of age. The between-individual component comprises both permanent environmental effects and a genetic component (Findlay and Cooke 1982). I calculated repeatability measures using the results of one-way analysis of variance applied to 1) egg size among females across years, 2) egg size among females across clutches within a year, and 3) date of first clutch initiation across years.

A three-way contingency table was constructed to observe the pattern of egg size ordering in successive years. The table was analyzed using log-linear models after the example of Fienberg (1970) and Bishop et al. (1975). In addition to testing the assumption of mutual independence which characterizes classical contingency analyses, the techniques of Fienberg can be used to calculate the frequencies of events that would be expected under all possible conditions of dependence (interaction) between two or more classifying variables. Goodness of fit tests are then used to determine which of a series of hierarchical models based upon various assumptions of dependence best explain the observed frequencies of the event (Harder 1980).

If social stimulation tends to promote synchrony in initiation of first clutches in neighbours (Makkink 1942), then females in a locality should tend to lay at more similar dates than females in different localities. One way to test for synchronization is to compare the variance of observed clutch initiation dates in an area (s_1^2) with the variance of observed clutch initiation dates for all other birds (s_2^2) and

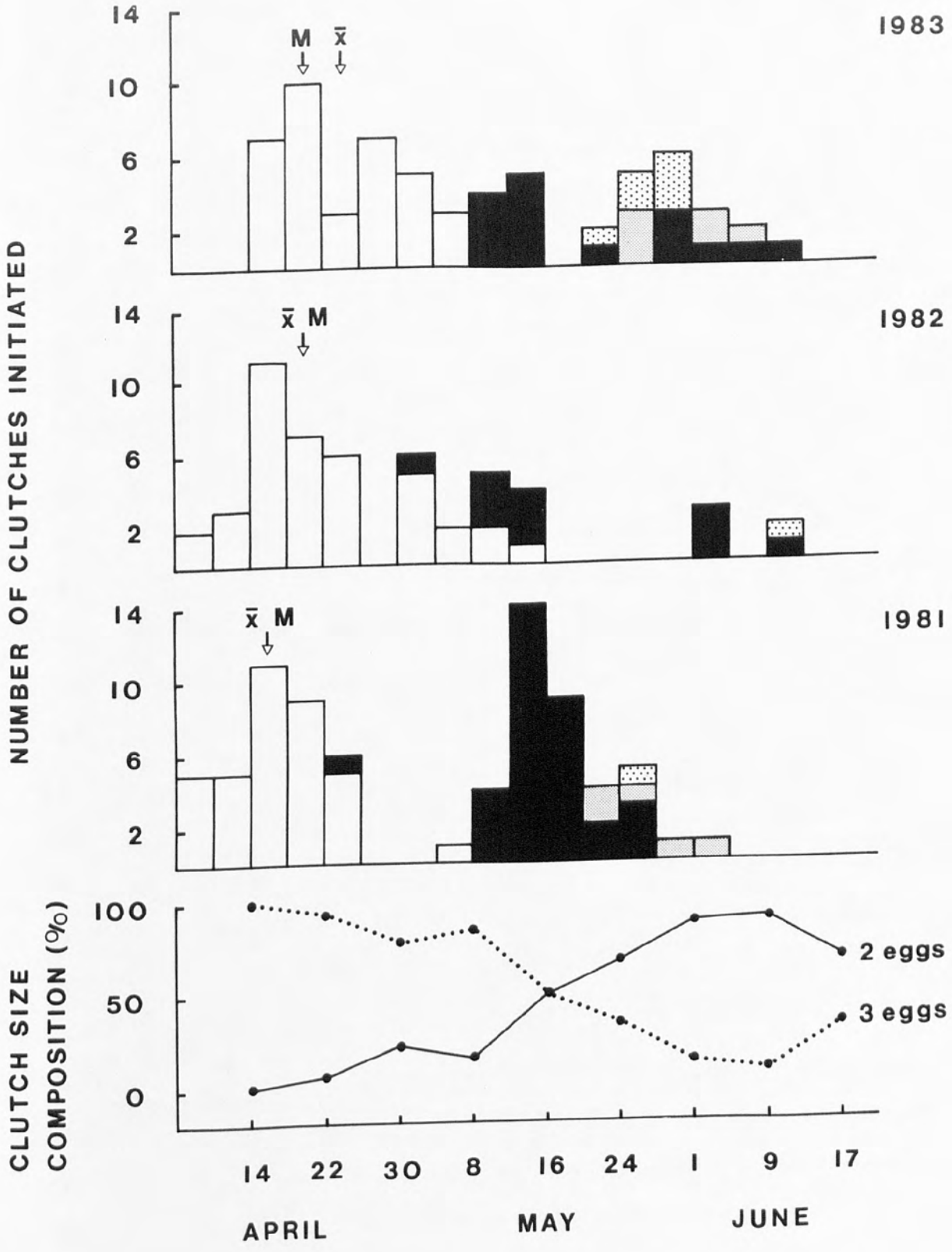
to compute the ratio of variances (s_2^2/s_1^2). I obtained 500 random partitions of the data into samples of size n_1, (the number of nests in the locality in question) and n_2 (the number of total clutches initiated in a year - n1), and computed the variance ratio for each, then looked to see if the observed value fell in the upper 5% tail of the distribution of 500 empirically obtained ratios (Sokal and Rohlf 1981).

3. Results

3.1. Clutch initiation

American Oystercatchers breeding in Virginia initiated clutches over a short period. Initiation dates of first clutches range from as early as 6 April (1981) to as late as 13 May (1982); however the mean spread of dates for 1981 to 1983 was only 25 days. The average date of initiation of first clutches for 1981 to 1983 was progressively later in the successive breeding seasons (Fig. 2). Frequency distributions of clutch initiation dates before 28 April are similarly shaped in the 1981 and 1982 breeding seasons. In 1983 the curve is flattened from an increase in the spread of clutch initiation dates and the mean date of first clutch initiation is slightly later. The 1983 field season was characterized by a cold, wet April and this most likely caused the shift in clutch initiation dates.

Fig. 2. Frequency histograms for 1981-83 breeding seasons showing number of first clutches (open bar), second clutches (black bar), third clutches (fine stippled bar) and clutches of unknown sequence (bold stippled bar). Location of mean ($\bar{x}$) and median (M) laying dates are indicated by arrows. The bottom panel shows the proportion of two and three egg clutches ($\underline{n}$ = 156).


NUMBER OF CLUTCHES INITIATED
14
10
6
2
M
x̄
1983
1982
1981
CLUTCH SIZE COMPOSITION (%)
100
50
0
2 eggs
3 eggs
14
22
30
8
16
24
1
9
17
APRIL
MAY
JUNE

The time of initiation of replacement clutches was related to the date on which the first clutch was lost. High spring tides occurred before the majority of females had laid and after eggs in the first clutch had hatched. In 1983 nests were lost to both spring tides and predation at about the same time. This pattern of nest loss resulted in a small second peak of laying from 5 to 12 May. The pairs represented by this peak lost their nest a second time to predation, all within four days, resulting in a third peak of laying in late May and early June (Fig. 2).

Approximately three quarters of the total variance in clutch initiation dates was explained by the effects of female and year. About 59% of the variation in clutch initiation dates was explained by variation between females ($P < 0.001$) and about 16% by variation between years ($P < 0.001$). The repeatability (r) measure for date of clutch initiation for those females that laid in three consecutive years was high (total phenotypic variance=97.8, r=0.73, n=22), and shows that females tend to lay at about the same time in each year. However, when examining the year to year correlations between clutch initiation dates it is clear that in 1983 females were less likely to lay at the same dates as in 1981 and 1982 (1981 to 1982, r=0.740, $P < 0.001$, n=22; 1982 to 1983, r=0.485, $P < 0.02$, n=23) and were also less likely to lay at the same dates relative to their neighbours (Spearman rank correlation coefficients: 1981 to 1982, r_s=0.816, $P < 0.001$; 1982 to 1983, r_s=0.463, $P < 0.02$). Again a cold wet April and persistent high tides in some nesting areas caused some females to lay at a later date in 1983 than in previous years, and this fact alone would lower the year to year correlation.

When known females on a territory attained new mates (n=4) in successive breeding seasons they still tended to lay at about the same date as in the previous year. However, in two instances when males retained their territories but acquired different mates in the subsequent breeding season, these new females laid 16 and 26 days later than the original residents.

Synchrony of clutch initiation dates for first clutches (as defined by a significant s_2^2/s_1^2 ratio, see methods) occurred in all five localities in at least one of the three years of intensive study (1981-1983). Females nesting on the sand spit of southern Wallops Island in 1982 showed more synchrony than the general population (6 nests, $\underline{P} < 0.05$). There was evidence for synchrony in all three years among the females on Chincoteague Point (9 nests, 1981, $0.05 < \underline{P} < 0.1$; 1982, $\underline{P} < 0.01$; 1983, $\underline{P} < 0.01$). At the north end of Wallops Island there was significant synchrony in 1983 (4 nests, $\underline{P} < 0.01$) but not in either 1981 or 1982. Synchrony was also detected in 1983 on Chincoteague Island (5 nests, $\underline{P} < 0.01$) and in 1981 on Assawoman Island (5 nests, $\underline{P} < 0.01$).

3.2. Clutch size

Average clutch size declined as the season progressed. Most first clutches in 1981 to 1983 contained three eggs (Table 1). About two-thirds of first replacement clutches (second clutch) contained two eggs. Second replacement clutches (third clutch) contained two eggs in all but three nests which contained three eggs each. In 1979, 42.4% of first clutches contained two eggs, and in 1978 one clutch (3.0% of all clutches) contained four eggs.

The proportion of three-egg clutches declined through the breeding season (Fig. 2) but females laid three-egg clutches as late as 1 June in 1981 and 2 and 13 June in 1983 (Fig. 2). Females normally lay a maximum of two replacement clutches when preceding clutches are lost, but one female laid three replacement clutches in 1979, although one and possibly two of these were incomplete. Females that laid replacement clutches in 1981 and 1983 tended to lay the same size clutches ($\chi^2=3.19$, d.f.=1, n=13, $0.05 < P < 0.10$).

TABLE 1. Clutch size of *Haematopus palliatus* on Chincoteague, Wallops and Assawoman Islands, Virginia in six breeding seasons, 1978-1983.

Year	n	Number of eggs in first clutch					Number of eggs in second clutch				Number of eggs in third clutch				Number of eggs in clutches of unknown number			
		1	2	3	4	u[1]	1	2	3	u	1	2	3	u	1	2	3	u
1978	33	0	1	2	1	0	0	0	0		0	0	0		2	9	18	
1979	43	1	14	18		0	1	3	4		0	1	1		0	0	0	
1980	18	0	0	0		0	0	0	0		0	0	0		2	6	10	
1981	83	1	2	31		6	1	17	11	5	0	4	1	3	0	1	0	
1982	54	0	4	31		6	0	9	1	2	0	1	0		0	0	0	
1983	63	0	4	19		13	1	8	6	1	0	6	1		1	2	0	1
Total	294	2	25	101	1	25	3	37	22	8	0	12	3	3	5	18	28	1

[1] u - clutches with unknown number of eggs

3.3. Egg size.

Egg size in the combined data set (including data for all eggs of known laying sequence, regardless of clutch number or clutch size) varied systematically with laying order (Table 2). On average the second laid egg was the largest (most voluminous) and the heaviest. The first and third eggs were about equal in volume. When I categorized the data according to clutch sequence I obtained a similar result. In first clutches (a sample of mostly three-egg clutches) the second egg was larger and heavier than the first ($P < 0.015$), and heavier than the third ($P < 0.015$). The first and third eggs were of equal size, but the third egg was longer ($P < 0.015$). In second clutches (a sample of two-egg and three-egg clutches) the second egg was also the largest ($P < 0.015$).

I then categorized the data by the size of the clutch. In three-egg clutches the second egg was largest and heaviest and the first and third eggs were equal in size and weight ($P < 0.015$). The second egg was longer than the first ($P < 0.004$) and wider than the third ($P < 0.011$). In two-egg clutches the second egg was largest ($P < 0.02$) and tended to be longer than the first ($P < 0.07$).

The pattern of egg-size ordering varied by year (Table 3). In 1982 the second egg was the same size as the first about half the time and there was no significant difference in their volumes. The log-linear model (Fienberg 1970) that best fits the overall pattern of egg-size ordering by year shows an interactive effect between year (Y) and egg

TABLE 2. Egg dimensions for first, second and third laid eggs of *H. palliatus* in Virginia.

	Egg sequence[1]			Eggs of unknown number
	1	2	3	
	(*n* = 116) $\bar{x} \pm$ S.E.	(*n* = 95) $\bar{x} \pm$ S.E.	(*n* = 69) $\bar{x} \pm$ S.E.	(*n* = 241) $\bar{x} \pm$ S.E.
Volume (cc)	41.68 ± 0.27^a	43.22 ± 0.27^b	42.28 ± 0.32^a	42.34 ± 0.18
Length (mm)	56.05 ± 0.21^a	57.09 ± 0.19^b	56.95 ± 0.20^b	56.31 ± 0.13
Breadth (mm)	39.46 ± 0.11^a	39.82 ± 0.11^a	39.43 ± 0.14^a	39.68 ± 0.07
Weight (g)	47.69 ± 0.42^a	49.65 ± 0.40^b	47.72 ± 0.53^a	49.30 ± 0.50

1 Homogeneous groups indicated with superscripts. Differences tested using Multiple t-tests ($P < 0.015$) following one-way ANOVA (Sokal and Rohlf 1969).

TABLE 3. Frequencies and standardized deviates[1] of clutches with first eggs of greater than and equal to, or less than volume of, second eggs in two- and three-egg clutches, from 1978 to 1983.

Year	Clutch size	Egg order		Total
		1 ≥ 2	1 < 2	
1978-79	Two-egg	1(-0.1)	3(-0.2)	4
	Three-egg	3(0.8)	5(-0.3)	8
1981	Two-egg	2(-1.1)	18(1.3)	20
	Three-egg	3(-1.7)	25(0.5)	28
1982	Two-egg	4(0.4)	4(-1.9)	8
	Three-egg	12(2.6)	16(-0.3)	28
1983	Two-egg	2(-0.1)	10(1.3)	12
	Three-egg	3(-0.4)	9(-0.7)	12
Total		30	90	120

1 Standardized deviates = (Obs - Exp)/ $\sqrt{Exp}$ for model of complete independence (Bishop et al. 1978).

size order (E), and an independent effect of clutch size (C) (Table 4). The standardized deviates, which indicate the deviation from the value expected based on the pattern observed in other years, are greater in three-egg clutches of the year 1982 (Table 3) than those expected by chance (Bishop et al. 1975). When the 1982 data for three-egg clutches with second eggs equal to or less than the volume of first eggs are removed, and replaced with structural zeros (Bishop et al. 1975) the simple three-factor model of no interaction (Y,C,E) becomes sufficient ($P < 0.05$) to explain the data. The proportion of clutches with no apparent egg size ordering was considerably higher in 1982 than in any other year.

Average egg volume did not differ between clutches of two and three eggs (Table 5). In a comparison of egg size in first and second clutches laid by the same female, volume, breadth, and weight were significantly lower in second clutches than in first, and most of the total variation was attributable to differences among females (Table 6). However, in a similar comparison for all clutches of known sequence, no differences in egg size between first and second clutches emerged, but length and volume were significantly lower in third clutches than in first or second clutches (first clutch: length 56.4± 1.86 mm, volume- 42.7 ± 2.19 cc; second clutch: length- 56.4 ± 1.86 mm, volume- 42.2 ± 2.37 cc; third clutch: length-55.1 ± 1.43 mm, volume-40.6 ± 2.14 cc, one-way ANOVA, $P < 0.015$ for differences as above).

Mean egg volume for each female was plotted with the date of clutch initiation and no apparent relationship was found (1981, r=0.13, n=25, $P < 0.05$; 1982, r=-0.16, n=23, $P < 0.05$), except in 1983 when volume was

TABLE 4. Values of the log likelihood ratios ($\underline{G}^2$) for selected models of interaction between clutch size (C), presence of egg size ordering (E) and year (Y), in the data from Table 3. For a given model, variables that appear together within commas were assumed to be jointly dependent, but the effect of that interaction is independent of the other specified interactions or single factor effects.[1]

Model	$\underline{G}^2$	d.f.	P
E,C,Y	19.99	10	< 0.05
EY	15.05	8	0.1 > P > 0.05
C,EY	6.41	7	n.s.
E,CY	14.16	7	< 0.05
Y,EC	19.21	9	< 0.05
EC,EY	5.63	6	n.s.
EC,EY,CY	0.53	3	n.s.

1 Probabilities less than 0.05 associated with models of equal or less complexity indicate their inability to provide adequate explanations of the data (Sokal and Rohlf 1981).

TABLE 5. Effect of clutch size on variation in egg size parameters.

Egg	Clutch size: 2-egg $\bar{x} \pm$ S.E. (n = 68)	Clutch size: 3-egg $\bar{x} \pm$ S.E. (n = 286)	P[2]
Volume (cc)	42.4 ± 0.29	42.8 ± 0.15	n.s.
Length (mm)	56.9 ± 0.25	56.6 ± 0.12	n.s.
Breadth (mm)	39.5 ± 0.14	39.8 ± 0.05	$0.1 > P > 0.05$
Weight (g)	48.7 ± 0.44[1]	48.7 ± 0.27	n.s.

[1] n = 39 for weights

[2] Differences tested by one-way ANOVA

TABLE 6. Effect of female, clutch sequence and year on variation in egg size parameters.

A. Clutch sequence
(n = 39 females)

Egg	First clutch $\bar{x}$	Second clutch $\bar{x}$	Variation attributable to: Female[a] R^2(%)	Female[a] F	Clutch sequence[a] R^2(%)	Clutch sequence[a] F
Volume (cc)	43.8	42.5	71.6	3.69***	9.0	17.67***
Length (mm)	56.7	56.3	76.1	3.38***	0.1	2.40
Breadth (mm)	40.2	39.8	74.5	4.05***	7.1	14.74***
Weight (g)	50.0	48.2	78.5	4.39***	2.8	4.79*

B. Year
(n = 24 females)

Egg	1981 $\bar{x}$	1982 $\bar{x}$	1983 $\bar{x}$	Variation attributable to: Female[a] R^2	Female[a] F	Year[a] R^2	Year[a] F
Volume (cc)	43.0	42.7	42.8	55.2	2.48**	.38	0.20
Length (mm)	56.7	56.6	56.7	84.6	11.04***	.07	0.09
Breadth (mm)	39.8	39.7	39.7	60.8	3.13**	.35	0.21
Weight (g)	48.4	48.6	50.3	55.1	2.18*	.09	4.00

a Significance levels designated as follows: *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$. Differences among means tested by two-way ANOVA of females with clutch sequence and year.

negatively correlated with date ($r=-0.39$, $n=29$, $P < 0.006$). This result probably reflects the larger number of second replacement clutches of lower average volume in 1983.

About 55% of the variation in egg size over the three years, 1981 to 1983, was attributable to differences among females, rather than differences among years (Table 6). There was no indication of a difference in egg size in any of the six years of the study ($P < 0.05$, one-way ANOVA with full data set). Females for which I have data for three to six years appear to lay eggs of about the same average volume, with no apparent change as a result of increasing age.

Repeatability estimates of egg characteristics over several years were available for 24 females (Table 7a). About 35% of the total phenotypic variance of egg volume in first clutches arises from differences between individuals. The remainder reflects intra-individual variation in response to fluctuating environmental conditions. Within a single season between 29 and 66% of the total phenotypic variance arises from differences between females (Table 7b), depending on the year and the egg character.

TABLE 7. Analysis of phenotypic variation in average egg size over several breeding seasons and over successive clutches in each breeding season.

A. Egg size over several breeding seasons ($\underline{n}$ = 24 females, 72 observations)

	Volume	Length	Breadth
Between-individual variance (Added variance component due to differences among females)	1560.77	2.28	0.326
Within-individual variance	2942.32	0.59	0.427
Total phenotypic variance	4503.09	2.87	0.753
Repeatability (r_a)	0.35	0.80	0.43

B. Egg size over successive clutches
1981 ($\underline{n}$ = 23 females, 48 observations)

	Volume	Length	Breadth
Between-individual variance	3410.46	1.89	0.43
Within-individual variance	3132.05	0.95	0.54
Total phenotypic variance	6542.51	2.84	0.97
r_a	0.52	0.66	0.44

1983 ($\underline{n}$ = 15 females, 37 observations)

	Volume	Length	Breadth
Between-individual variance	1116.23	1.64	0.47
Within-individual variance	2788.20	1.70	0.28
Total phenotypic variance	3904.43	3.34	0.75
r_a	0.29	0.49	0.63

3.4. Female size

Females were heavier than males (females, $\bar{x}$ = 638±42 g , n=30, males, $\bar{x}$ = 567±113 g, n = 30, t = 2.75, $P < 0.01$). Average egg volume (EV) ranged from 35.85 cc to 45.18 cc ($\bar{x}$±s.e.; 41.94 ±0.504). To test for a relationship between female size and egg volume (EV) I first used body weight as an index of size. Body weight and EV were correlated significantly (r=0.47, $P < 0.05$, n=19). However, body weights of oystercatchers are known to fluctuate markedly in the breeding season, especially around the egg laying period (Mercer 1968). I therefore also tested for a correlation between EV and the geometric mean (GM) of eight external body measurements, (Mosimann 1970, Mosimann and James 1979), which is free of short-term seasonal bias. Female size as represented by GM is correlated significantly with EV, (r=0.508, $P < 0.025$) but accounts for only 4% more of the variation in egg volume than does weight. Using either body weight or the GM of body measurements it is apparent that larger females tend to lay more voluminous eggs than smaller ones, although clearly female size was not the only factor affecting egg size. Similar analysis of male measurements and weights revealed no influences from male size on egg size.

4. Discussion

Most first clutches in the study area were initiated within a 20-day period in all intensively studied breeding seasons (1981 to 1983). The oystercatchers I studied were slightly less synchronous in the spread of initiation dates for first clutches than a population of breeding Willets (Cataptrophorus semipalmatus) found nearby (Howe 1982, Table 8) but more synchronous than H. moquini in South Africa and H. ostralegus in Scotland (Table 8). As expected, shorebirds nesting at higher latitudes are more synchronous in clutch initiation dates than American Oystercatchers (Table 8), although interspecific differences in nesting synchrony cannot be accounted for solely on the basis of latitude differences (e.g., H. ostralegus vs. H. palliatus).

Social stimulation probably affects laying dates in oystercatchers. Birds within localities had lower variances in the dates of initiation of their first clutches than did the general population in the study area. Synchrony within localities was most consistent where the largest numbers of oystercatchers nested (Chincoteague Point). Oystercatchers are very vocal and aggressive towards neighbouring pairs, frequently participating in long piping displays in the pre-laying period and this extensive piping may stimulate egg laying in some females. Consistent differences in environmental factors affecting females in different localities probably do not explain this finding as neighbouring pairs of oystercatchers used widely differing foraging sites and these differences were as large as the differences between sites (Nol in preparation). The high repeatability estimate obtained here is confounded by

TABLE 8. Comparison of ranges of nest initiation dates in eleven species of shorebirds.

Species	Mean No. of Observations	Range (No. of days)	Location	Comments	Reference
American Oystercatcher (Haematopus palliatus)	28	25	37°50′N,75°30′W	Mean of 3 years	This study
Black Oystercatcher (Haematopus bachmani)	8 17	21 24	48°38′N,123°17′W 48°18′N,123°32′W	Total of 5 years	Drent et al. (1964)
African Black Oystercatcher (H. moquini)	55	84	33°05′S,17°57′E	1 year	Hockey 1983
European Oystercatcher (Haematopus ostralegus)	45	42	51°42′N,5°16′W	Mean of 3 years	Keighley & Buxton (1948)
Black-bellied Plover (Pluvialis squatarola)	3	5.5	75°40′N,84°35′W	Mean of 4 years	Hussell & Page (1976)
Willet (Catoptrophorus semipalmatus)	80	21	37°40′N,75°20′W	Est. (by Nol), 2 yrs., replacement clutches not identified	Howe 1982
Ruddy Turnstone (Arenaria interpres)	13	13	81°49′N,71°18′W	1 year	Nettleship 1973
Western Sandpiper (Calidris mauri)	58	26	61°30′N,64°50′W	Mean of 3 yrs., repl. clutches not identified	Holmes 1972
White-rumped Sandpiper (Calidris fuscicollis)	6	12.5	68°40′N,101°59′W	Mean of 2 years	Parmelee et al. (1968)
Dunlin (Calidris alpina)	12 18	9 22	61°31′N,64°50′W 61°30′N,21°40′E	Mean of 3 yrs Mean of 5 yrs	Holmes 1971 Soikkeli 1967
Stilt Sandpiper (Calidris himantopus)	14	14	58°45′N,93°00′W	Mean of 3 yrs Range estimated from hatching dates	Jehl 1973

the effect of social stimulation and no inference about a heritable component can be made.

Most replacement clutches contained two eggs. With some exceptions, most clutches initiated after 3 June contained two eggs. The average volume of eggs in later clutches was smaller and this is probably a result of food limitations later in the season. Similarly, in Red-billed Gulls (Larus novaehollandiae), in New Zealand, egg volume and clutch size declined as the season progressed, and in that case, the decline appeared closely related to the decline in the amount of food (swarms of planktonic euphausiids) over the breeding season (Mills 1979). The food of the American Oystercatcher does not fluctuate as rapidly as do zooplanktonic populations but possibly is reduced enough through their own predation (O'Connor and Brown 1977) to affect both the size and number of eggs in replacement clutches.

Females tend to lay the same size replacement clutch from year to year. This consistency in clutch size over several years probably results from consistent differences in territory quality among females, rather than from a genetic component. Birds in poor territories may be contributing a greater proportion of their total energy reserves to a three-egg first clutch and then can only lay a two-egg replacement clutch, whereas birds occupying richer feeding territories can lay a second three-egg clutch. This is currently under study (see Chapter 4).

Over a third of the yearly and annual variation in egg size arose from the between-individual component of the total phenotypic variation. At least part of this component is attributable to the effect of female size. A high repeatability in egg size from year to year has been found

in at least six species of shorebirds (Väisänen 1969, Väisänen et al. 1972, Miller 1979), in Darwin's finches (Geospiza spp.)(Grant 1982), and in Great Tits (Parus major; Ojanen et al. 1979, Van Noordwijk et al. 1981). In at least some species egg size has also been found to be heritable (Great Tit, Van Noordwijk et al. 1981; Red Grouse (Lagopus lagopus scoticus; Moss and Watson 1982).

Within-clutch ordering of egg size in shorebirds has received considerable attention, primarily because eggs laid last in other Charadriiformes (notably larids) are usually smaller, and this pattern may have considerable adaptive significance (Coulson 1963, Parsons 1970, Gochfeld 1977, Lundberg and Väisänen 1979). However, the literature on shorebird egg size is confusing because of the apparent equation of increased size with increased length or breadth. In American Oystercatchers an increase in length does not necessarily influence volume, and therefore size of an egg. In those studies where researchers found an increase in only one of the components of volume with laying sequence (e.g., Miller 1979, Nol and Lambert 1984) egg size as measured by volume has usually remained constant (e.g., Cairns 1977). Thus a special explanation for the adaptiveness of egg-size ordering in most shorebirds with four-egg clutches need not be sought.

In American Oystercatchers, the first egg is smaller than the second egg, but about equal to the third egg in three-egg clutches, and smaller than the second egg in two-egg clutches. Eggs hatch in the order that they are laid. There are at least three hypotheses to explain the adaptive significance of egg-size ordering, but most explain only consistent increases or decreases in egg size over the laying sequence

(vis. larger later eggs because of increased predation of incomplete clutches, Warham 1974, Miller 1979, Clark and Wilson 1981; higher provisioning in later laid eggs enhancing competitive position of those chicks in the case of hatching asynchrony, Howe 1976; smaller, later eggs as a form of brood reduction, Parsons 1975, Gochfeld 1977, Braun and Hunt 1983).

The explanation for the larger second egg in clutches of the American Oystercatcher may reside with the different risks to each of the eggs. Incubation is commenced after the second egg is laid (pers. obs.) and thus for the initial two days the first laid egg is exposed to increased risk of loss from predators and environmental fluctuations. The probability of loss for the first egg is likely to be higher than that for the eggs in an incubated clutch (Miller 1979). Although eggs hatch in the order they are laid, the first two eggs hatch relatively synchronously and the resultant young may leave the nest before the third egg has hatched. Disturbance from predators or other sources can cause the parents to abandon the third egg to attend the hatched young. The second egg therefore may have the highest probability of survival, and this could account for the pattern of egg-size ordering within clutches.

The magnitude of egg size differences (4% by volume) in American Oystercatchers is small compared to those in most larids (10-30% of volume, see Parsons 1970, Davis 1975, Nisbet 1978, Lundberg and Väisänen 1979) but similar to that recorded in Roseate Terns (Sterna dougallii) late in the breeding season (Nisbet and Cohen 1975). In American Oystercatchers fresh egg weight and weight of young at hatching are corre-

lated ($r=0.82$, $n=8$, $P < 0.025$), the heaviest chick coming from the second egg. Within broods the differences in chick weights parallel those among egg weights, unlike Black-legged Kittiwakes (Rissa tridac tyla) where asynchronous hatching markedly enhances weight differenc within the brood once all chicks have hatched (Braun and Hunt 1983).

Even relatively small differences in egg size can result in a sibling social hierarchy. A sibling social hierarchy in H. palliatus similar to that described previously for H. ostralegus and H. bachma (Safriel 1981, Groves 1984). When a parent arrives with food one chi rushes towards the parent while the others remain crouched or standi with the second parent. If the other chicks run to be fed, the domi chick turns and chases its siblings. Only when the dominant chick se satiated does the next in rank emerge to be fed. In European Oyster-catchers (H. ostralegus) the social hierarchy among chicks in a broo follows the weight hierarchy at hatching (Safriel 1981), and it is p able that this is also true in H. palliatus.

The social hierarchy facilitates brood-reduction during periods low food availability because subordinate chicks either starve or ar eliminated by predators (Safriel 1981). In periods of food abundance chicks in the brood can be fed. As well, the sibling hierarchy might promote a more efficient distribution of food if less of the parents and chicks' energy is wasted during sibling competition (Hamilton 19 Hahn 1981). This advantage alone might provide an impetus for parent manipulation of egg size independent of the predictability of resour

Chapter 3: SEX ROLES IN THE AMERICAN OYSTERCATCHER

1. Introduction

Most species of birds are monogamous (Welty 1962, Lack 1968). However, the quality and quantity of the contributions by each sex to parental care, often appear, or are assumed to be unequal (Willson and Pianka 1963, Trivers 1972, Alexander 1974, Alcock 1975, Dawkins 1976). Trivers' (1972) concluded that differential investment by each sex in their offspring was 'molded' from the initial differential gametic contribution of the sexes. The parent with the least invested in the offspring would be favoured by natural selection to desert (Trivers 1972). This idea remains largely unchallenged today, in part because it predicts the structure of parental behaviour so well in terms of individual selection. Gladstone (1979) disagreed with the shape of Trivers' cumulative investment curves when considering monogamous colonial species in which there was documented evidence for forced extra-pair copulations. In these species Gladstone concluded that the curves of both parents should be more or less equal because the pre-copulatory costs for males in territorial defence, nest building, and courtship displays should be as high as the costs for females of producing eggs. Males should be more likely to desert if cuckoldry is suspected because then their genetic contribution to the brood will be smaller than the females.

Although agreeing in principle with Trivers' conclusions, Dawkins and Carlisle (1976) emphasized the importance of future expectations rather than past expenditure in determining the selective value of desertion by the parent with the least investment. This was expanded in mathematical terms by Maynard Smith (1977), who devised a simple model to predict when it would pay for one or the other parent to desert. The deserter gains nothing by desertion unless it can find another mate, so that the degree of breeding synchrony and hence probability of finding an unmated bird in a population must be accounted for in predicting any evolutionarily stable strategy (Maynard Smith 1977). Recently Burger (1981) suggested that, in monogamous birds, the contribution of the male would be greater than that of the female because the male would expend a great deal of energy guarding the female to prevent cuckoldry. Several workers have found that during the pre-laying period males invest heavily in territorial or mate defence (Montevecchi and Porter 1980, Mock 1979, Pierotti 1981).

Recent interpretations of sexual differences in parental behaviour are based on Trivers' (1972) premise that the relationship between the sexes during the breeding season involves an ongoing assessment by each member of the pair of their respective contributions (Mock 1979, Gladstone 1979, Montevecchi and Porter 1980, Pierotti 1981), and that each sex attempts to maximize the care its mate provides while minimizing its own contribution. The inherent conflict between the sexes falls on a continuum of intensity ranging from those species where offspring are easily raised by one parent (no cooperation) to species where biparental care is required to raise the young (high degree of apparent cooperation). Trivers (1972) termed the apparent cooperation as

'complementarity' of sex roles.

Natural selection should act to favour an efficient use of energy by the parents which results in the greatest genetic contribution to future generations (Fisher 1958). The need for energetic efficiency will underlie the structure of the apparent cooperation between members of the pair. Unbalanced contributions by either sex to parenting should be interpreted as differences in levels of energetic efficiency in performing different tasks. Conflict between the sexes would be predicted for circumstances where energetic stresses affect the adults (e.g., food shortages).

The young of the American Oystercatcher (Haematopus palliatus) require extensive parental care, and adults therefore should have sex roles based on apparent cooperation. In this chapter I define and measure the breeding season sex roles of the American Oystercatcher in terms of time and energy expenditure. The objective is to compare cumulative energy expenditure curves for males and females. The chapter has the following structure: I compare time budgets in each of the four stages of the breeding season to determine the degree of concordance between members of a pair. I then analyze the pattern of foraging during chick-rearing to examine the underlying structure of cooperation between mates. Members of a pair can either forage alternately to provision the young, or they can take a number of trips proportional to the relative energetic costs of foraging by each bird. Through an examination of the patterns of anti-predator, territorial, and foraging behaviour in provisioning the young, I attempt to describe the apparent 'cooperation' between the sexes, and determine whether sex roles in oystercatchers are

related to the reverse sexual dimorphism in size (see Chapter 2). Sex roles of the American Oystercatcher are then described multivariately, to determine the degree of similarity in time budgets between the sexes. I then construct energy budgets of males and females over the breeding season to test the fit of the actual curves of breeding season energy expenditure with theoretical parental investment curves for monogamous species (Trivers 1972, Gladstone 1979).

2. Methods

2.1. Study area

Oystercatchers were studied on Wallops and Assawoman islands, (37°50 N, 75°35 W), the dredge spoil areas west of these islands, and the salt marshes and dunes around the Chincoteague Channel, Chincoteague, Virginia (37°55N, 75°23W). Birds were observed for a period of 14 months over 3 breeding seasons (March-July 1981, April-July 1982, March-July 1983).

Habitats on Assawoman, northern Wallops Island and Chincoteague Point were characterized by sand dunes and pebbled beaches, with predominant vegetation of beachgrass (Ammophila breviligulata). The predominant vegetation of dredge spoils and salt marshes consisted of Spartina alternifolia and Disticylus spichata, and small stands of Iva frutescens and Baccharis halimifolia. Nest sites on the dredge spoils and in the salt marshes were surrounded by S. alternifolia, Salicornia virginica,

and Cakile edentula in various stages of growth.

2.2. Estimation of time budgets

Observations were made from blinds set on the study areas, from offshore boats or across channels from a distance of at least 30 m from the nests, using a 20 X Bushnell Spacemaster telescope. From each location I was able to observe from two to seven pairs simultaneously. Individuals were banded with aluminum bands and unique colour-band combinations.

Observational data were collected in 10-min continuous-observation focal-animal sampling sessions (Altmann 1974) within 4 to 6 hour periods. During chick-rearing the sampling periods ranged from 0.85 h to 12 h of continuous observations.

Birds were chosen randomly for sampling during these periods. The periods were systematically chosen with respect to the time of the day. On each successive day sampling began 4 to 6 h later at a different phase of the tide. This resulted in all birds being observed at different times of the day and at different phases of the tide. Although this sampling scheme produced an unequal number of samples of each bird it had the advantage that each bird was sampled in each division of daylight hours and each stage of the tide (i.e., ebb, low, flood, and high tide). The exact nature of the effect of the tide cycle on the behaviour of American Oystercatchers is given elsewhere (Chapter 4).

Data were collected in the pre-laying, laying, incubation and chick-rearing stages. For subsequent analyses the pre-laying and chick-rearing stages were divided into early and late periods (early pre-laying: before 31 March, late pre-laying: 31 March to egg laying, and all pre-laying periods before renesting; early chick-rearing: before 1 June; late chick-rearing: 1 June and later). During the first three of these stages I collected data using an electronic event decoder (International Instruments Inc.). Pulses generated by the decoder were amplified and recorded on a Uher tape recorder. I coded 57 behavioural categories which I was able to record without removing my eye from the eyepiece of the telescope. The event decoder provided a record of the time of occurrence for all behavioural categories. The resulting tapes were played back into a computer in the Department of Zoology, Universsity of Toronto, and condensed and organized through a series of customized programmes.

The 57 behavioural categories were reduced to 22 by (1) contextual criteria (e.g., standing or sitting with head back after a long period of standing quietly, with no intruders nearby were condensed to the category resting), and (2) by running a transition matrix of the raw data through a multidimensional scaling programme (MDS) (Spence 1979). Categories appearing in similar positions in a three-dimensional space were condensed into one. For example, all preening activities had similar coordinates on all three axes of the MDS solution and thus I felt justified in considering any act of preening as simply preening. The matrix contained only those categories which I was not able to categorize by contextual criteria (e.g., shake head, scratch head, bob, etc.). The final categorization of behaviours is as follows: (1) Resting:

Standing or sitting with head turned back and bill resting on back feathers. (2) Preening: Manipulating feathers with the bill. (3) Standing: Standing without head turned back. (4) Walking: Walking around without pecking at food items. (5) Searching for food and foraging: Walking while pecking and feeding. (6) Piping: The territorial display of the American Oystercatcher (Miller and Baker 1980), performed in flight or on the ground. (7) Sitting: Sitting without head back. (8). Bathing: Splashing water on feathers and preening while standing in water. (9) Brooding: Includes all nest directed activities: nest building, incubating or brooding chicks. (10) Feeding chicks: Presenting, and breaking up food for chicks. (11) Flying: Any flight except flights to and from feeding areas. (12) Crouching: Bending legs slightly to an almost sitting posture. (13) Number of piping displays: The frequency of piping. One piping display was considered terminated if there was a lapse of greater than 10 sec since the last act of piping. (14) Bobbing: Bobbing includes a summation of the frequency of each act of head up, look-up, bob, and single alarm notes. (15). Shaking: Shaking includes a summation of the frequency of each act of shake head, shake body, stretch leg, shake foot, scratch head, rub head, and yawn. (16) Chasing other species: Chasing or attacking any animal except conspecifics. Intruders or potential predators included Willets (Catrotrophorus semipalmatus), Fish Crows (Corvus ossifragus), Northern Harriers (Circus cyaneus), and Laughing Gulls (Larus atricilla). I considered chasing other species as anti-predator behaviour. (17). Chasing other oystercatchers. (18). Chased by oystercatchers: Being chased or attacked by conspecifics. (Total number of chases equals the sum of the number of (16), (17), and (18) above). (19) Drinking: Drinking. (20) Off terri-

tory. The bird was seen to fly toward a feeding area, and while there was assumed to be feeding. Off territory is analysed as a separate variable from searching for food, the latter being foraging time only around the nesting territory. Off territory is assumed to equal feeding in all stages but chick-rearing. During chick-rearing I was always able to see birds leaving and returning with food and have therefore categorized these trips separately: (21) Number of foraging trips: The number of foraging trips while feeding chicks. (22) Length of foraging trips: The total amount of time spent away from the territory on a foraging trip during the chick-rearing period.

2.3. Estimation of energy budgets

Basal metabolic rates (BMR) were calculated separately for males and females using the equation of Aschoff and Pohl (1970) for non-passerines. Daily energy expenditure (DEE) of each sex was calculated by summing the product of the amount of time spent in each activity by the energetic cost of that activity in kj. I then took the mean of the DEE for all individuals for each sex sampled on each day. The following caloric values were assigned to each activity: Resting = 1.24 x BMR (Aschoff and Pohl 1970); Preening = 2.5 x BMR; Standing = 1.5 x BMR; Walking = 2.8 x BMR (Maxson and Oring 1980); Searching for food = 3 x BMR (Orians 1961, Custer and Pitelka 1972); Piping = 9.3 x BMR (similar to fighting in Actitis macrularia, but less vigorous, Maxson and Oring 1980, birds spent about 60% of piping on ground and 40% in air. 9.3 x BMR is based on these proportions); Sitting = 1.24 x BMR (Aschoff and 1970); Bathing = 2.5 x BMR (similar to preening); Incubation and brooding = 1.14 x BMR

(females), 1.16 x BMR (males) (Ricklefs 1974); Feeding chicks = 3 x BMR (similar to feeding chicks); Flight = 5.5 x BMR (females), 5.2 x BMR (males) (Hart and Berger 1972, cost of flight for females was multiplied by 1.06 to account for the 6% larger wing loading of female oystercatchers (2.41 g/cm^2, 2.28 g/cm^2, $t=3.48$, $P < 0.001$). Crouching = 2.5 x BMR (similar to preening); Bobbing = 2 x BMR (between the values for preening and standing); Shaking = 2.5 x BMR (similar to preening); Total number of chases = 5 X BMR (Orians 1961, King 1974); Foraging trips = 3 x BMR (Orians 1961, Custer and Pitelka 1972). The cost of egg laying was taken as 8.9 kj / g wet weight (Ricklefs 1974).

Cumulative mean daily energy expenditure curves were constructed separately for each sex by plotting cumulative DEE for 37 successive days in the pre-laying period, 10 days in the laying period, 26 successive days in the incubation period, and 53 successive days in the chick-rearing period, corresponding to the approximate length of each stage respectively. I often had data for many more days in each stage, so I arbitrarily chose the days that corresponded to the average dates of those stages for the population. This resulted in the inclusion of those days for which I had sampled the largest number of individuals, and therefore had the most accurate estimate of DEE.

In addition to the continuous-observation sampling I also observed 28 pairs of Oystercatchers during the pre-laying period for lengthy periods (4.5 to 10 h) and recorded the behaviour and location (on or off territory) every 10 minutes in a scan sampling scheme (Altmann 1974). These scan samples were done to measure the degree of concordance between the behaviour of a bird and that of its mate. If the birds were

off the territory, they were usually seen previously flying to their feeding territories. I considered that mates were behaving similarly if both members of the pair were sitting, standing, or preening, or both members were out of view, presumably both on the feeding territories. The pairs were considered to be behaving differently if one member was out of view and the other was in view, or they were both observed simultaneously performing different activities.

2.4. Statistical methods

Time-budget data were tested for normality using the Kolmogorov D statistic (Sokal and Rohlf 1981). If the data were found to be skewed, arcsin (for percentage data), and square-root transformations (for frequency data) were applied (Sokal and Rohlf 1981). Since most data were still skewed after the transformations I used the Kruskal-Wallis distribution-free test on the transformed data to test for positive effects of either sex within each stage of the breeding season, or stage of the breeding season within each sex.

Data on the number and duration of foraging trips were normally distributed so standard parametric tests were used on untransformed data. Data on anti-predator behaviour were skewed, with a preponderance of zeros, so Spearman's rank correlation coefficients were used to test for relationships between members of a pair. Standard canonical discriminant analysis on transformed time budget data was used to describe sex roles (Pimentel and Frey 1978). Briefly, this analysis examines all behavioural variables simultaneously and calculates which

variable or combination of variables best describe differences between the sexes or stages of the breeding season (see Cooley and Lohnes 1971).

Additional analyses included the use of Pearsons correlation coefficient to test for correlations between morphological characters within a pair (i.e., assortative mating). A three-way contingency table was constructed to observe the pattern of provisioning the young by each sex and by different pairs. The table was analyzed using a log-linear model (Fienberg 1970). This analysis calculates the frequencies of events that would be expected under all possible conditions of interaction using the classifying variables. In all analyses P-values < 0.05 were taken to be significant.

3. Results

3.1. Sampling effort

A total of 1254 bird-hours of continuous observations were made during the pre-laying, laying, incubation and chick-rearing stages of the breeding season on from 18 to 42 individuals (Table 1). For the most part different individuals were sampled every year. In the following analyses individuals are used as sampling units. I omitted from the total sample all individuals for which I had fewer than 10 samples of 10-min observations.

TABLE 1. Sampling effort expressed as number of focal-animal samples and total number of hours observed by sex and stage of breeding cycle.

	Sex	Number of birds	Number of 10-min samples	Mean time (h)	Total number of hours	Range of number of hours/ bird
Prelaying	F	26	402	2.5	67	0.75-5.2
	M	27	384	2.2	64	0.70-5.8
Laying	F	19	384	3.5	64	0.76-7.5
	M	16	312	3.1	52	0.80-9.1
Incubating	F	26	456	2.8	76	0.72-6.4
	M	24	390	2.5	65	0.73-5.3
Chick-rearing	F	19	- [1]	22.1	421	0.85-105.3
	M	23	- [1]	19.3	445	0.85-104.7

1 During chick-rearing sampling periods were continuous and varied from 0.85 h to 12 h.

3.2. Nesting and Feeding areas.

Oystercatchers defend a territory that usually contains suitable nesting habitat with piping and some fighting. Nesting territories only rarely contain extensive areas with abundant suitable food. Most birds fly from 100 to 1000 m to traditional feeding areas where they may or may not defend the area around them against other oystercatchers. Aggressive interactions on the feeding areas were usually brief compared to those on the nesting areas. In the following time budgets feeding time is defined as all time off the nesting territory although it is possible that birds did not always feed while off the territory. It was never possible for me to follow individual birds to the feeding areas when they left the nesting territories. However, observations on the feeding areas suggest that birds spent most of their time there feeding.

3.3. Time of day differences.

I tested whether time of day had a significant effect on the time budgets of breeding oystercatchers. Females stood for slightly less time in the morning than in the afternoon or evening during the incubation stage. They fed more during the afternoon during incubation, but showed no diel pattern in their behaviour during the chick-rearing stage. During incubation, males also fed more frequently in the afternoon. In the chick-rearing stage males brooded the chicks less during the afternoon than the morning or evening. There were no other differences in behaviour by time of day for either sex.

3.4. Sex differences.

The proportion of time spent by either sex in each activity and the frequencies of activities were compared within each stage of breeding. During pre-laying the behaviour of males and females was similar for all activities (Table 2). Individuals showed a high degree of concordance between their own behaviour and that of their mates. In 3326 of 3603 scans (92 %) both members of a pair were behaving similarly, and in 277 (8 %) each member of the pair was behaving differently.

I analysed whether this similarity of behaviour between the sexes occurred both early and late in the pre-laying period, because the later period should contain the actual period of follicle formation (Ricklefs 1974). A rough estimate of the length of this period for renesting American Oystercatchers was about 10 days (n = 8). During the early

TABLE 2. Proportion of time spent and frequency of activities by male and female American Oystercatchers during the pre-laying stage.

Activity[1]	Females (n = 26)	Mean[2] rank	Males[2] (n = 27)	Mean rank	Significance[3]
Resting	27.0	27.5	28.0	26.5	n.s.
Preening	10.0	23.6	11.0	30.3	n.s.
Standing	25.0	28.0	25.0	26.0	n.s.
Walking	7.0	26.3	7.0	27.7	n.s.
Searching for food	15.7	29.5	12.7	24.6	n.s.
Piping	1.0	29.6	0.7	24.5	n.s.
Sitting	10.0	28.0	10.4	26.1	n.s.
Bathing	0.3	25.9	0.3	28.1	n.s.
Incubating/brooding	2.0	26.7	2.1	27.3	n.s.
Flying	1.8	28.9	1.3	25.2	n.s.
Crouching	0.2	27.2	0.2	26.9	n.s.
No. of piping	0.07	28.0	0.07	26.0	n.s.
Bobbing	0.2	29.0	0.2	25.1	n.s.
Shaking	0.15	25.5	0.17	28.5	n.s.
Chase others	0.003	24.9	0.009	29.0	n.s.
Chase oystercatchers	0.002	25.3	0.005	28.7	n.s.
Chased by oysterc.	0.0007	26.5	0.002	27.5	n.s.
Drinking	0.0008	27.5	0.00	26.5	n.s.
Total no. of chases	0.005	24.6	0.016	29.3	n.s.

1 Numbers represent percentages when data based on proportions, and number of acts/100 sec, when data are based on frequencies.

2 Rank is Wilcoxon's rank sum.

3 n.s. means not significant.

pre-laying period females spent slightly more time searching for food and piping than did males ($P < 0.09$, Fig. 1). Late in pre-laying there were no differences between the behaviour of males and females. Significant differences between early and late pre-laying were found in seven activities of females and five activities of males (Fig. 1).

During the laying period males stood more than females, tended to crouch less, and chased other oystercatchers more (Table 3). During incubation, the number of differences in the time-budgets between the sexes increased. Males rested more, preened more, sat more, flew slightly more, incubated less, performed more comfort movements, and chased oystercatchers more than females (Table 4).

During the chick-rearing period the behaviour of the sexes was again similar (Table 5). Males performed all activities except chasing at about the same frequency or duration as females. Males chased and were chased by other oystercathers and were involved in more chases overall than were females.

Fig. 1. Time spent in different activities by males and females early (stippled bars) and late (open bars) in the pre-laying stage. Only activities resulting in significant differences are shown.

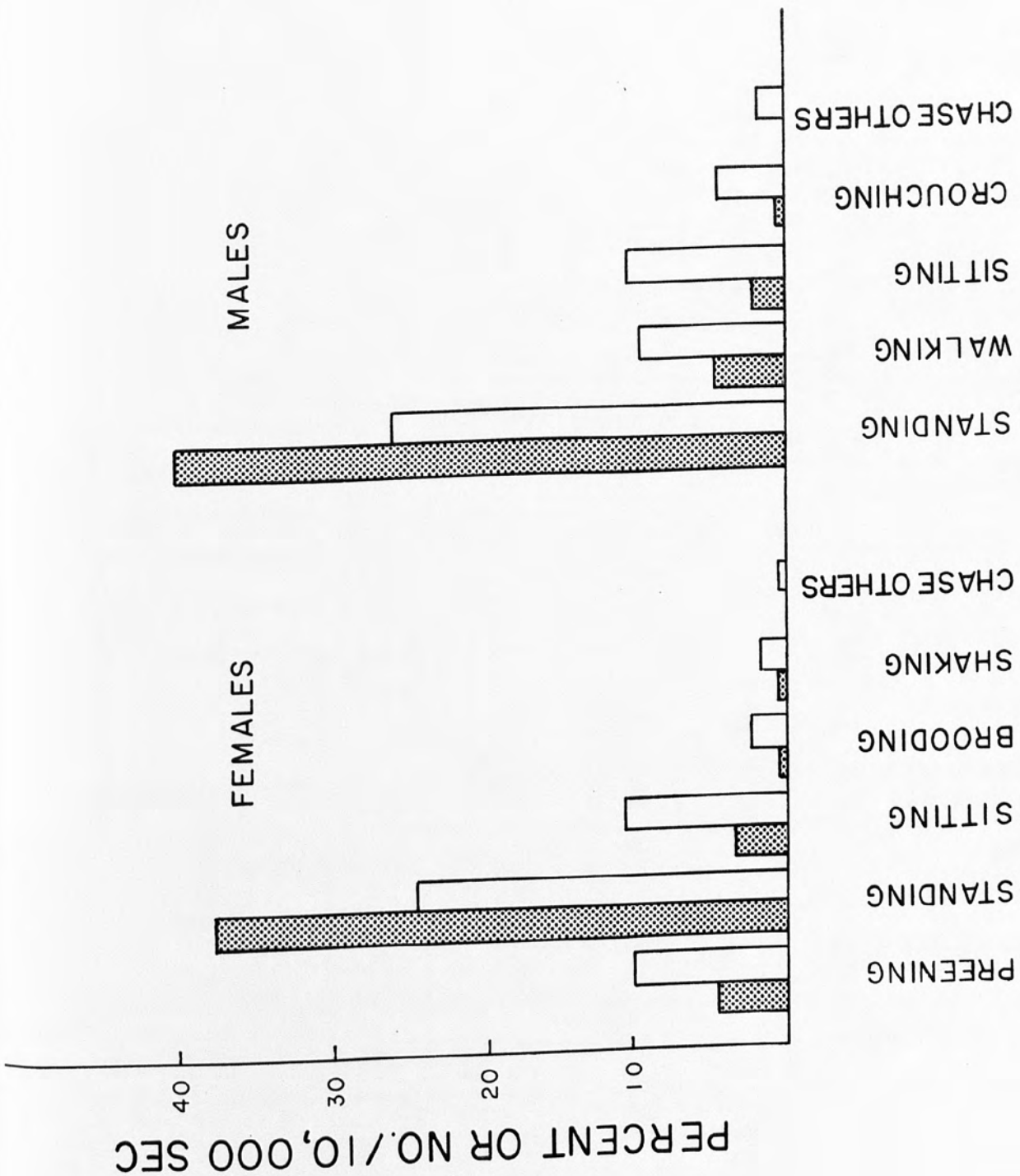

PERCENT OR NO./10,000 SEC
40
30
20
10
FEMALES
PREENING
STANDING
SITTING
BROODING
SHAKING
CHASE OTHERS
MALES
STANDING
WALKING
SITTING
CROUCHING
CHASE OTHERS

TABLE 3. Proportion of time spent and frequency of activities by male and female American Oystercatchers during the laying stage.[1]

Activity	Females (n = 19)	Mean rank	Males (n = 16)	Mean rank	Significance
Resting	13.6	17.7	13.6	18.3	n.s.
Preening	7.1	16.6	9.7	19.7	n.s.
Standing	15.9	14.9	24.4	21.7	P <0.0527
Walking	5.2	15.7	7.7	20.7	n.s.
Searching for food	18.8	16.8	22.2	19.4	n.s.
Piping	0.9	17.3	1.0	18.8	n.s.
Sitting	5.2	19.1	2.4	16.7	n.s.
Bathing	0.2	17.2	0.3	18.9	n.s.
Incubating/brooding	38.8	20.5	26.3	15.0	n.s.
Flying	0.7	16.4	1.0	19.9	n.s.
Crouching	0.8	20.3	0.07	15.3	P <0.089
No. of piping	0.04	16.8	0.05	19.4	n.s.
Bobbing	0.07	20.0	0.08	15.6	n.s.
Shaking	0.05	16.5	0.08	19.8	n.s.
Chase others	0.004	16.2	0.015	20.1	n.s.
Chase oystercatchers	0	15	0.016	21.6	P <0.0044
Chased by oystercatchers	0	17.5	0.0012	18.6	n.s.
Drinking	0	18.4	0	17.5	n.s.
Total no. of chases	0.004	15.1	0.033	21.5	P <0.038

1 Superscripts same as in TABLE 2.

TABLE 4. Proportion of time spent and frequency of activities by male and female American Oystercatchers during the incubation stage.[1]

Activity	Females (n = 26)	Mean rank	Males (n = 24)	Mean rank	Significance
Resting	5.5	20.7	8.9	30.7	P <0.016
Preening	7.2	20.7	13.4	30.7	P <0.016
Standing	14.4	22.8	15.8	28.5	n.s.
Walking	5.3	24.5	5.7	26.6	n.s.
Searching for food	9.2	23.7	12.4	27.4	n.s.
Piping	0.8	24.8	0.9	26.3	n.s.
Sitting	1.5	21.9	4.4	29.4	P <0.058
Bathing	0.1	22.7	0.3	28.5	P <0.072
Incubating/brooding	56.9	31.3	38.7	19.2	P <0.0036
Flying	1.0	23.5	1.1	27.6	n.s.
Crouching	0.2	23.9	0.2	27.3	n.s.
No. of piping	0.16	24.3	0.07	26.8	n.s.
Bobbing	0.06	24.8	0.17	26.3	n.s.
Shaking	0.20	21.1	0.32	30.3	P <0.028
Chase others	0.01	27.0	0.01	23.8	n.s.
Chase oystercatchers	0.004	20.4	0.02	31.0	P <0.003
Chased by oystercatchers	0.0002	23.9	0.0045	27.2	n.s.
Drinking	0.034	25.8	0.028	25.2	n.s.
Total no. of chases	0.0165	22.8	0.027	28.5	n.s.

[1] Superscripts same as in TABLE 2.

TABLE 5. Proportion of time spent and frequency of activities by male and female American Oystercatchers during the chick-rearing stage.[1]

Activity	Females (n = 19)	Mean rank	Males (n = 23)	Mean rank	Significance
Resting	2.8	22.4	2.8	20.8	n.s.
Preening	3.9	23.4	2.7	20.0	n.s.
Standing	37.4	23.2	31.4	20.1	n.s.
Walking	5.3	20.7	5.9	22.2	n.s.
Searching for food	24.7	21.9	23.2	21.2	n.s.
Piping	2.2	19.5	2.6	23.1	n.s.
Sitting	4.7	22.5	6.9	20.7	n.s.
Bathing	0.05	22.3	0.3	21.7	n.s.
Brooding	7.9	24.1	3.1	19.4	n.s.
Flying	0.65	20.8	0.8	22.0	n.s.
Crouching	0.45	22.9	0.23	20.4	n.s.
No. of piping	0.064	20.1	0.081	22.7	n.s.
Bobbing	0.029	19.9	0.044	22.8	n.s.
Shaking	0.029	22.6	0.025	20.6	n.s.
Chase others	0.0097	20.9	0.010	22.0	n.s.
Chase oystercatchers	0.0068	18.2	0.018	24.2	$\underline{P}$ <0.084
Chased by oystercatchers	0.0057	18.2	0.014	24.2	$\underline{P}$ <0.079
Drinking	0.0043	22.1	0.0037	21.0	n.s.
Total no. of chases	0.022	17.8	0.042	24.5	$\underline{P}$ <0.054
Feeding chicks	7.8	20.7	7.9	22.2	n.s.

1 Superscripts same as in TABLE 2.

3.5. Feeding trips.

I observed foraging trips of 19 pairs, but for the following analyses I use only data from 10 pairs for which I have greater than 10 foraging trips during the chick-rearing period. Foraging trips are assumed to be the most costly of activities for American Oystercatchers because of the distances flown to feeding areas and because these trips are frequent during the chick-rearing stage.

The pattern and frequency of foraging trips might be expected to differ if the pair is engaged in a conflict over raising the young, or if the relationship within the pair is based on apparent cooperation. For example, if, after each foraging trip to provision the young, the male hesitates before leaving for the next trip in anticipation that the female will take the initiative and leave, and if the female, after returning employs the same strategy, then the system should fixate at alteration of foraging trips (i.e., a simple 'tit for tat' model, Axelrod and Hamilton 1981). This result should occur only if there is a cost associated with leaving the young unattended. The cost provides the incentive for a 'returner' to return before the 'leaver' leaves due to its own food stress.

On the other hand if energetic considerations determine the parents' pattern of foraging for the young then the number of trips by males and females should be adjusted so as to minimize overall energy expenditure by each member of the pair and to maximize the amount of food brought back to the chicks. In the following analyses I assume that males and females forage with equal intensity. I compare the length

of the foraging trips, the number of trips per sampling period, and the length of time since the last foraging trip by the returner and the leaver.

The length of time between the return of a male from a foraging trip and the leaving of a female (M-F) is shorter than the opposite pattern of a returning female followed by a leaving male (F-M)(Table 6). The time between two successive trips by the male (M-M) is about one-third longer than the time between two successive trips by the female (F-F)(Table 6). The time between successive trips is more variable for females than for males (S.D.; F-F trips, 1.88, M-F trips, 2.02; M-M trips, 1.81, F-M trips, 1.82). Regardless of which member of the pair took the previous trip the male waits longer before leaving on his trip than does the female. For females the length of the wait also is not dependent on who took the previous trip. These results suggest that it is internal motivation rather than past events which trigger when a bird will leave on a foraging trip. Overall, males make about 25% more foraging trips per unit time than do females (Table 6). Males also make slightly longer foraging trips than do females (Table 6).

I then analysed the distribution of feeding trips within an observation period (Table 7). M-M trips predominated and F-F trips were higher than the number expected by chance (log-linear model, Fienberg 1970), and this pattern was more or less consistent among pairs. This result suggests that trips by males and by females were clumped in time. I then plotted the rate of trips by each sex as a function of the time of day. Females made proportionally more trips later in the day than did males. Males appeared to spread the timing of their trips evenly

TABLE 6. Lengths of foraging trips, rate of foraging trips and lag intervals between trips for male and female American Oystercatchers (mean).

Variable	Males (n = 548)	Females (n = 363)	Significance[1]
Trip length (min)	10.17	9.09	P <0.068
Trip rate (# trips/100 min feeding time)	2.4	1.9	P <0.054
Lag since last trip (min) by same sex (min)	15.41[2]	11.99[3]	P <0.039
Lag since last trip by mate (min)	13.37[2]	9.59[3]	P <0.0007
Lag since last trip (min)	14.34	10.91	P <0.078

1 Significance tested with Wilcoxon two-sample test.

2,3 Significant differences between values indicated by different superscripts.

TABLE 7. Number of foraging trips during the chick-rearing stage, preceded by same sex, or opposite sex in 10 pairs of oystercatchers.

		Trip followed by:	
Pair	Trip preceded by:	Male	Female
A4	Male	9	8
	Female	9	13
I1	Male	20	3
	Female	4	4
I4	Male	12	13
	Female	12	8
20	Male	58	33
	Female	32	34
N2	Male	14	8
	Female	7	5
PD	Male	20	13
	Female	13	18
PE	Male	37	31
	Female	32	21
PF	Male	48	22
	Female	16	13
PG	Male	33	17
	Female	16	18
18	Male	23	11
	Female	12	7
Total	Male	274	159
	Female	153	141

$\chi^2 = 9.44$ $P < 0.005$

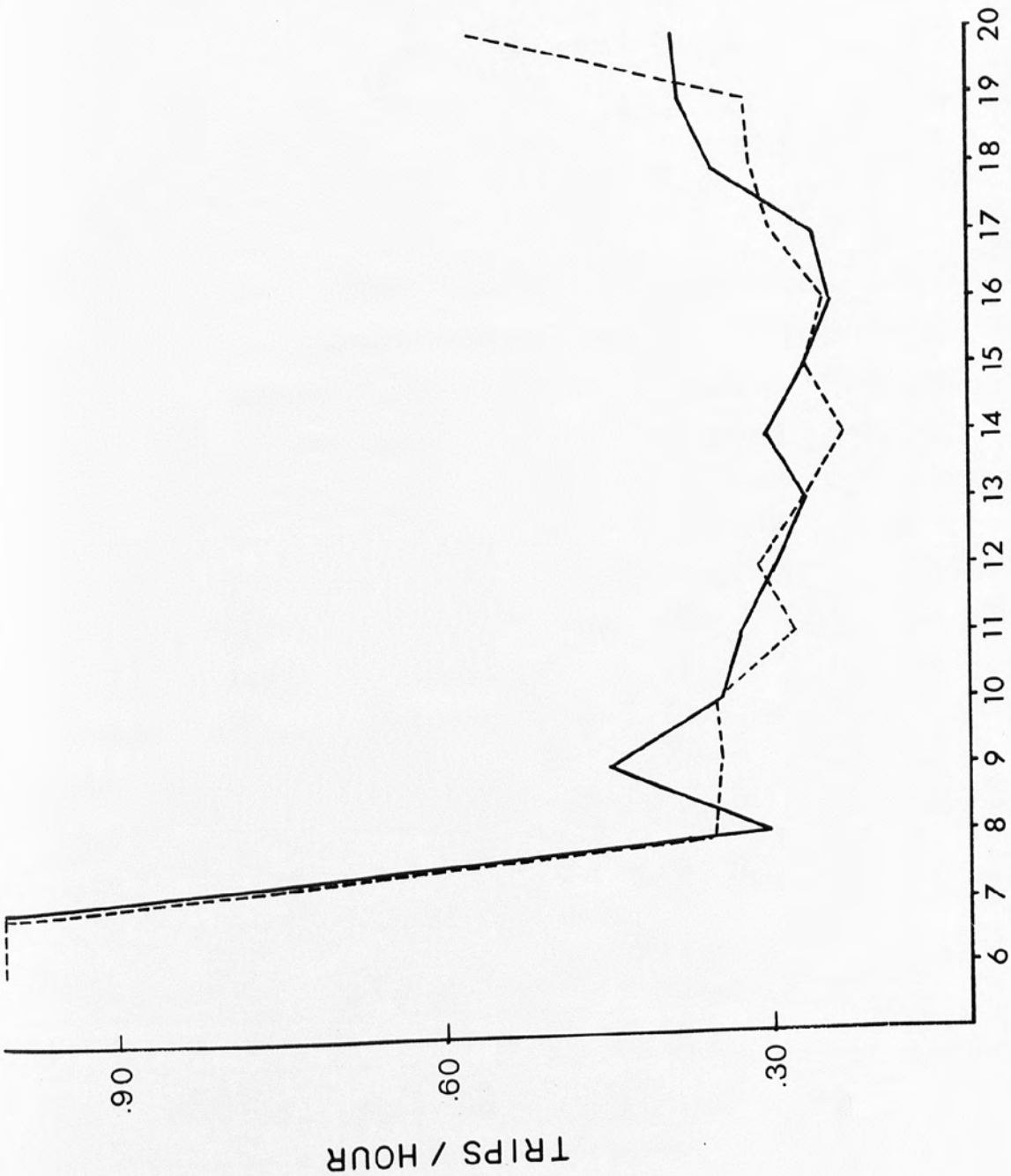
throughout the day, with the exception of early in the day when both males and females made the greatest number of trips (Fig. 2). Within all pairs observed, males made more foraging trips than females.

3.6. Anti-predator and territorial behaviour.

3.6.1. Anti-predator behaviour - 'cooperative' model.

If both members of a pair have an equivalent 'interest' in preventing nest predation and if participation by both members is more likely to cause predators to find the nest (as in incubation), then one would expect the member of the pair that contributes less to incubation to chase more and there should be no correlation between the occurrence of chasing by one member of the pair and the occurrence of chasing by its mate. During chick-rearing there should be no difference in the number of chases of potential predators between the sexes, and a positive correlation between the occurrence of chasing by one member of the pair, and chasing by its mate. The results for these correlations are presented below.

Fig. 2. Average hourly rates of foraging by males (solid lines) and females (broken lines) to provision the young. Time is based on a 24 h clock.


.90
.60
.30
TRIPS / HOUR
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
TIME (h)

3.6.2. Anti-predator behaviour - 'uncooperative' model.

By contrast, if members of the pair have different interests then during incubation and early in chick-rearing before chicks are fully mobile there should be a correlation between the occurrence of chasing by one bird and the occurrence of chasing by its mate. This should be true if the risk of predation of the eggs or brood is higher when there is no attempt to chase off predators, than when the predators are being chased off and the eggs or brood are uncovered. During chick-rearing when there is little brooding, but a high risk of predation (after the chicks are mobile) the correlation by occurrences of chasing between mates should be high, because regardless of their motivation, each bird will benefit from adequate protection of young from predators. As the chicks get older and the risk declines, then there should be less correlation between members of the pair, and a large variance in chasing behaviour as one or the other member tries to minimize their respective contributions.

3.6.3. Territorial behaviour - 'cooperative' model.

During incubation, if both members of a pair have an equal interest in preventing intrusions by conspecifics on their territory and if the occurrence of territorial acts does not affect the probability of loss of young to predators then there should be a correlation between the occurrence of territorial acts by one member of the pair and the occurrence of these acts by its mate. During chick-rearing, if parental contributions are equal, then territorial acts should be equal and the occurrences correlated. If, however, the chick-rearing contributions are unequal, the parent that has 'more time' should contribute more to territorial activities than its mate.

3.6.4. Territorial behaviour - 'uncooperative' model.

If members of the pair have unequal interests during incubation then there should be no correlation in the frequency of their territorial behaviour, providing that the function of the territory is to protect a mate (e.g., from cuckoldry). Conversely, there should be a strong correlation if the function of the territory is to protect a nest site, because this behaviour is clearly in the interests of both members of the pair. During chick-rearing, if the function of territorial behaviour becomes less important there should be little correlation in behaviour of members of a pair. Each sex should avoid territorial behaviour if the mate is there to do it, and on average each sex should engage in it equally, but not simultaneously.

Correlations to measure the joint participation in the same activities by mates were computed pairwise for the three categories of chasing behaviour, piping, the number of piping displays and bobbing in the incubation and chick-rearing stages. Spearman's rank correlation coefficients between the frequency of acts given by males and females during a single sampling session are given in Table 8. Correlations between members of the pair were significant and high for all acts when the pair had chicks. During incubation, correlations were significant only for piping, number of piping displays and bobbing. Each member of the pair appeared to act independently when chasing conspecifics or potential predators. These results support the pattern of correlations predicted by the equal-interest models (sections 3.6.1 and 3.6.3).

3.7. Effect of stage of breeding.

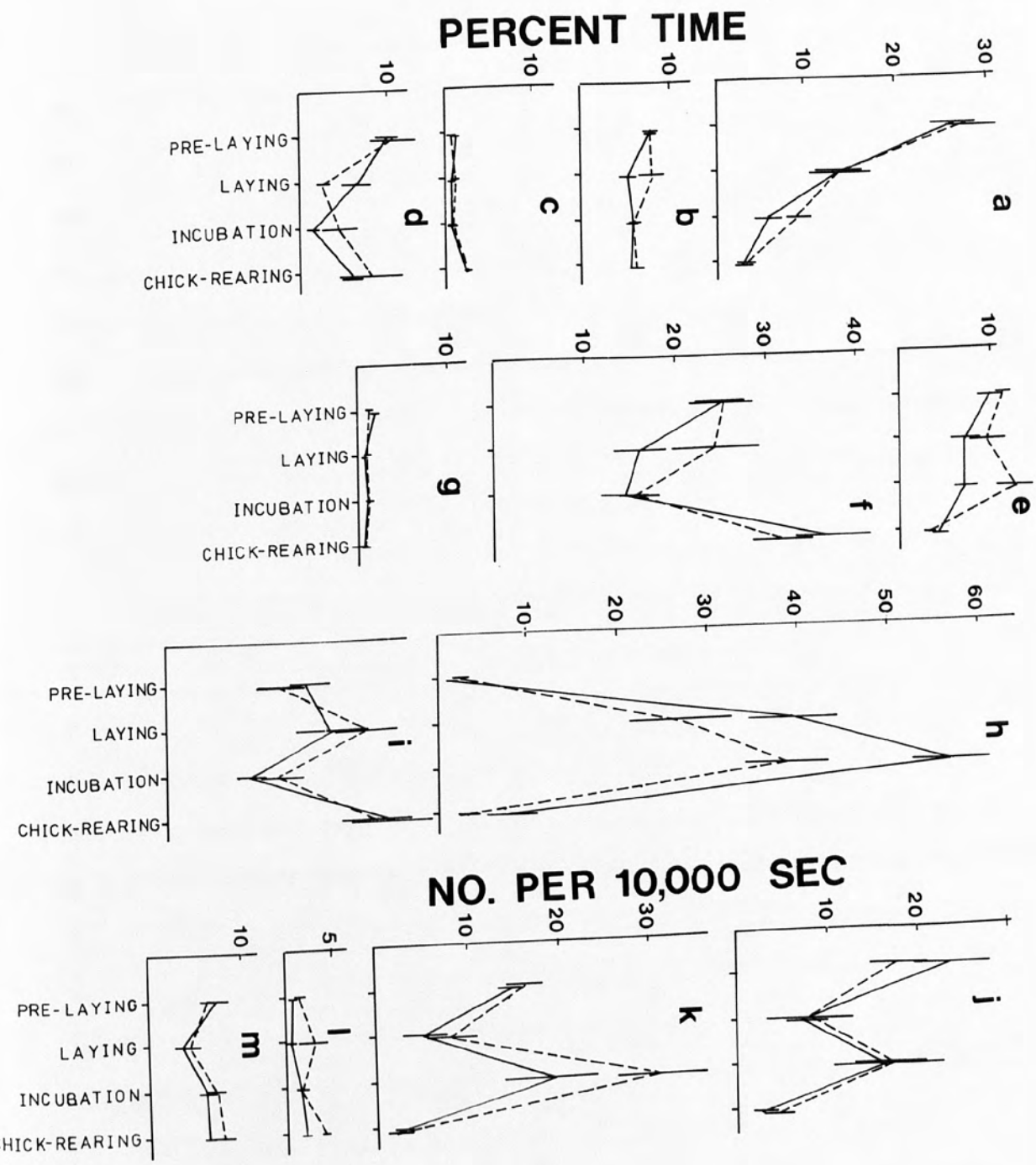
For females, the time spent in every activity except the amount of time spent walking changed over the course of the breeding season (Fig. 3). For males, walking, the number of piping displays, and the number of chases directed at other species all stayed constant and occurred randomly over the four stages of the breeding cycle. This latter fact lends some credence to the assumption that the number of potential predators in the study area remained roughly constant over the breeding cycle.

TABLE 8. Spearman rank correlation coefficients within pairs of the American Oystercatcher on the incidence of territorial and anti-predator behaviour during incubation, and early and late chick-rearing stages.

Activity		Incubation (n = 133)	Early chick-rearing (n = 117)	Late chick-rearing (n = 85)
Bobbing	r	0.35	0.55	0.75
	P	0.001	0.0001	0.0001
Piping (sec)	r	0.21	0.70	0.81
	P	0.014	0.0001	0.0001
Number of piping displays	r	0.18	0.60	0.73
	P	0.036	0.0001	0.0001
Chasing non-conspecifics	r	-0.09	0.38	0.46
	P	n.s.[1]	0.0001	0.0001
Chasing conspecifics	r	0.04	0.41	0.31
	P	n.s.	0.0001	0.0043
Chased by conspecifics	r	0.00	0.40	0.22
	P	n.s.	0.0001	0.0441
All chases	r	0.10	0.27	0.27
	P	n.s.	0.0037	0.0134

[1] n.s. means not significant.

Fig. 3. Time spent and frequency of activities in four stages of the breeding season by male (dashed lines) and female American Oystercatchers (solid lines). Activities are coded as follow: resting (a), walking (b), piping (c), sitting (d), preening (e), standing (f), flying (g), brooding (h), searching for food (i), bobbing (j), shaking (k), chases (l), and no. of piping (m).


PERCENT TIME
NO. PER 10,000 SEC
PRE-LAYING
LAYING
INCUBATION
CHICK-REARING
a
b
c
d
e
f
g
h
i
j
k
l
m

3.8. Multivariate descriptions.

To discuss sex roles strictly in relation to time spent in one activity without regard to preceding, concurrent or following activities oversimplifies the definition of a sex 'role'. A sex role should be viewed as a complex interaction of the full behavioural repertoire of an individual. For example high negative correlations were found between incubating and sitting because the activities are mutually exclusive. Hence it is misleading to look at each component of the time budget in isolation. Therefore I have chosen to describe the sex roles through multivariate analysis, which considers all variables simultaneously (Cooley and Lohnes 1971).

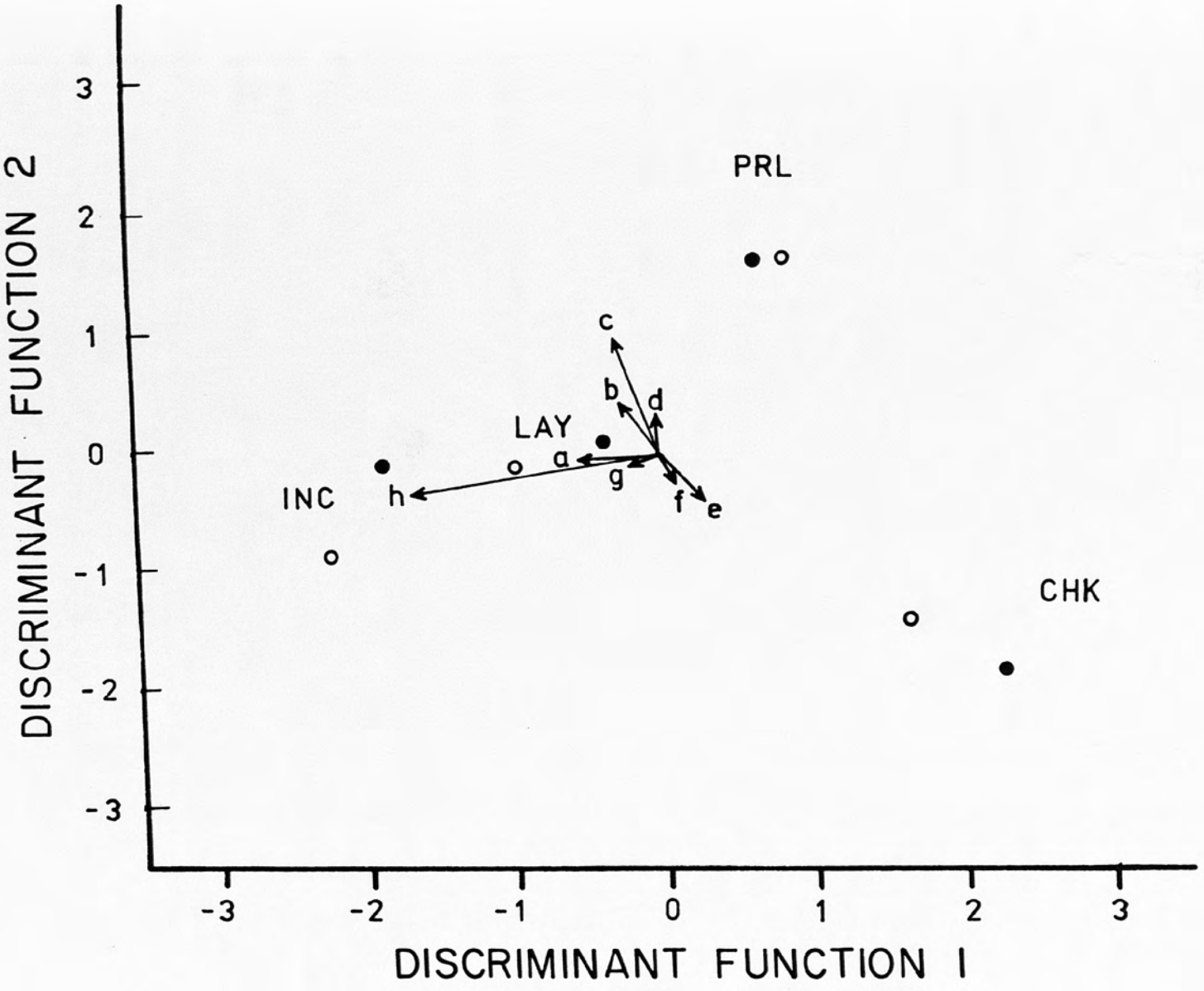
Examination of the Mahalanobis' distances among groups illustrates that differences between the sexes at any stage were less than those within each sex from one breeding stage to the next (Table 9). All distances except that between pre-laying males and pre-laying females were significantly different from zero. The distance a female 'travels' in multivariate space from the pre-laying to the laying stage (2.52 units) is not much greater than the distance travelled by the male (1.79 units). Intuitively it would seem that females are making a bigger transition because of the demands of egg laying. Males, however, begin assisting in incubation as soon as the females start to incubate (after the laying of the second egg), and males then consistently perform the same proportion of incubation throughout this breeding stage. Hence the males' place in discriminant space is also affected by the onset of laying (Fig. 4). The largest change in position occurs between incubating and chick-rearing birds of either sex. This is because the proportion of

TABLE 9. Mahalanobis distances between centroids of sex and stage of breeding groups, and associated probabilities for equality.[1] Stages of the breeding season are indicated as prelaying (P), laying (L), incubation (I) and chick-rearing (C).

	P♂	P♀	L♂	L♀	I♂	I♀	C♂	C♀
P♂	0	-	-	-	-	-	-	-
P♀	0.94	0	-	-	-	-	-	-
L♂	1.79***	2.09***	0	-	-	-	-	-
L♀	2.45***	2.52***	1.45	0	-	-	-	-
I♂	2.84***	3.01***	1.92	1.82	0	-	-	-
I♀	3.63***	3.80***	2.56***	1.84	1.81***	0	-	-
C♂	3.76***	3.82***	3.86***	4.32***	4.64***	5.05***	0	-
C♀	3.38***	3.34***	3.25***	3.52***	4.12***	4.32**	1.51	0

1*** - $P < 0.0001$, ** - $P < 0.001$, * - $P < 0.01$

Fig. 4. Plot of group centroids of male (solid circles) and female (open circles) American Oystercatchers showing sex roles during pre-laying (PRL), laying (LAY), incubation (INC) and chick-rearing (CHK). Vectors indicate the relative importance of individual variables to the sex roles. Variables are identified as follows: shaking (a), preening (b), resting (c), bobbing (d), piping (e), chased by oystercatchers (f), standing (g), incubating/brooding (h).


DISCRIMINANT FUNCTION 2
3
2
1
0
-1
-2
-3
PRL
c
b
d
LAY
a
g
INC
h
f
e
CHK
-3
-2
-1
0
1
2
3
DISCRIMINANT FUNCTION I

time in nearly all activities for each sex changes considerably (Tables 4 and 5). The positions of each group plotted in discriminant space (Fig. 4) also illustrates that distances among stages are always greater than the distances between the sexes at any one stage.

When group centroids and the variable vectors are plotted on the first two canonical axes, it is possible to determine which variable contributes most to the position of the group in discriminant space. The vectors orient in one of three directions (Fig. 4). The vectors for incubation, comfort movements and standing all orient toward incubating birds. Resting, preening and bobbing and the vectors representing piping and being chased by other oystercatchers separate chick-rearing birds from those incubating or pre-laying. Only preening, resting and piping make substantial contributions to group separations.

3.9. Sexual dimorphism.

Female American Oystercatchers on average weigh about 19% more than males (see Chapter 2). In all other mensural characters, females are significantly larger (unpublished data). American Oystercatchers do not seem to mate assortatively with respect to size. Of 13 Pearson correlations computed on characters of mated birds, none were significantly correlated between members of a pair. The plots of the values of each character by pair were examined. It was clear that each sex was as likely to be mated with a bird with a large measure of a particular character, as a small. Only for the character bill length did all 15 females have larger bills than their mates.

Differences in morphology between males and females may account for differences in the time budgets between the sexes. The energetic costs of most activities are measured as a multiple of the basal metabolic rate (BMR) expressed as kj/unit time. Since BMR is derived from weight, then the BMR of females will be greater than that of males, and hence for most activities the cost in kj per unit time will be greater for females. The cost expressed as a multiple of the BMR will usually be similar for each sex. However, the costs of incubation and flying (and all activities involving flying) depend on a multiple of BMR but are mediated by a range of other variables which effect the efficiency of performing those activities. The energetic cost of incubation is a negative power of body weight and includes the cost of raising the temperature of the clutch from ambient (taken here as 20^{o} C) to 35^{o} C. Consequently it is slightly more expensive for a male to incubate a clutch of 150 g (three eggs, see Chapter 2) than it is for a female. Conversely, the cost of flight depends on relative wing loadings (g/cm2). The lower the wing loading, the more efficient is flight. Males have a significantly lower wing loading than do females (see methods). This difference in efficiency (6%) is multiplied by the cost of flying at a certain body weight, to get the relative costs of flying by males and females. The relative costs of various activities (Table 10) were compared with the amount of time spent in these activities (Tables 2-5). During incubation males incubate 18% less than females. The cost of incubation for males is 2% more than the cost for females. Males make 26% more foraging trips to provision the young than do females (Table 6), and the cost of flight for males is 15% less than for females. Therefore only part of the difference in sex roles can be accounted for

TABLE 10. Costs (in kj/14 hr) of activities by male and female American Oystercatchers, used in constructing energy expenditure curves. The multiple of the basal metabolic rate (BMR) is in parentheses.

Cost (kj/14 hr)	Males	Females
Resting	146.7 (1.24)	160.1 (1.24)
Preening	295.9 (2.5)	323.1 (2.5)
Standing	177.7 (1.5)	193.9 (1.5)
Walking	331.1 (2.8)	361.6 (2.8)
Searching for food	354.9 (3.0)	387.5 (3.0)
Piping	1100.2 (9.3)	1201.3 (9.3)
Sitting	146.7 (1.24)	160.1 (1.24)
Bathing	295.9 (2.5)	323.1 (2.5)
Incubating/brooding	137.1 (1.16)	148.1 (1.14)
Flying[1]	1758.9 (14.9)	2012.3 (15.6)
Crouching	295.9 (2.5)	323.11 (2.5)
Bobbing	236.6 (2.0)	258.3 (2.0)
Shaking	295.9 (2.5)	323.11 (2.5)
Chasing	1758.9 (14.9)	2012.3 (15.6)
Drinking	295.9 (2.5)	323.11 (2.5)
Out of view/Foraging trips	354.9 (3.0)	387.5 (3.0)
BMR	118.3	129.2

1 The amount of time spent flying includes the length of time to fly to and from foraging areas.
$\bar{X}$ = 35.3 ± 14.8 sec. N = 14 territories.

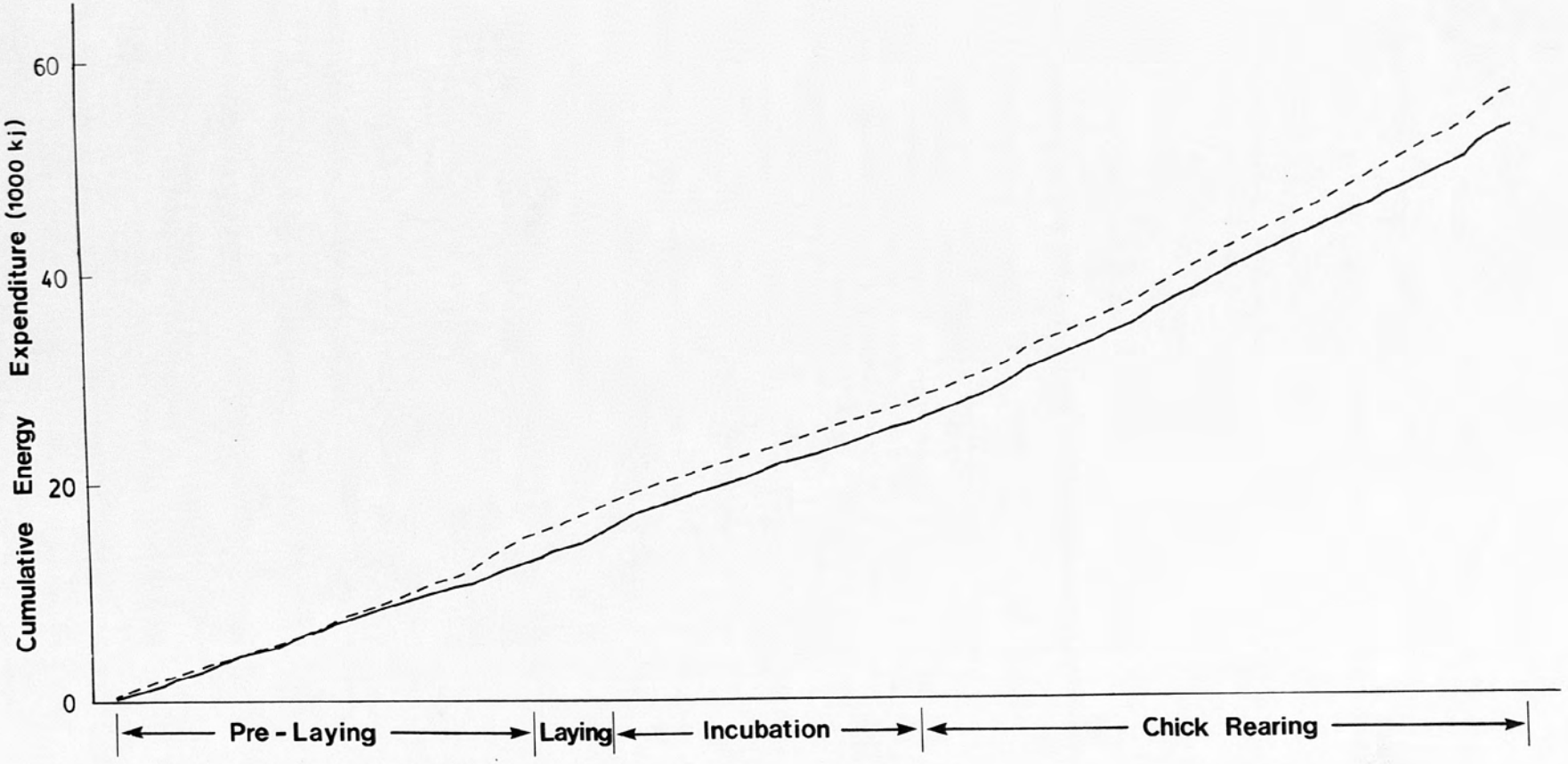
by differences in the costs of these activities for each sex.

3.10. Energy expenditure over breeding cycle.

Parental investment was measured using energy expenditure as an index. I have converted the time budget data to costs in terms of kj/day, and accumulated the daily energy expenditure over the breeding season (Fig. 5). In so doing I have attempted to duplicate Triver's original cumulative investment curves for monogamous species (Trivers 1972, p. 145). Two assumptions underlie these curves: the first is that cumulative energy expenditure is a measure of parental investment, and second, every act a bird does during the breeding season is related to fledging offspring. Presumably these assumptions are appropriate for all birds that spend time on a nest territory, rather than time simply feeding or resting (as in non-breeding birds).

In examining the curves it is clear that large differences do not occur between the sexes at any stage of the breeding cycle. As was reported above, the sexes expended about equal amounts of energy towards their future offspring during pre-laying. Just prior to the estimated time of follicle formation, the rate at which females expended energy appeared to go up relative to males, and by the end of the laying period females had expended about 16% (17985 vs 15569 kj) more energy than males, mostly due to the costs of egg laying. This 16% difference in 'investment' is maintained until the start of incubation when males raise slightly their rate of energy expenditure and by the end of incubation the difference between males and females has narrowed to about

Fig. 5. Cumulative daily energy expenditure (kj) for male (solid line) and female American Oystercatchers (dashed line) over the breeding season.


Cumulative Energy Expenditure (1000 kj)
60
40
20
0
Pre - Laying
Laying
Incubation
Chick Rearing

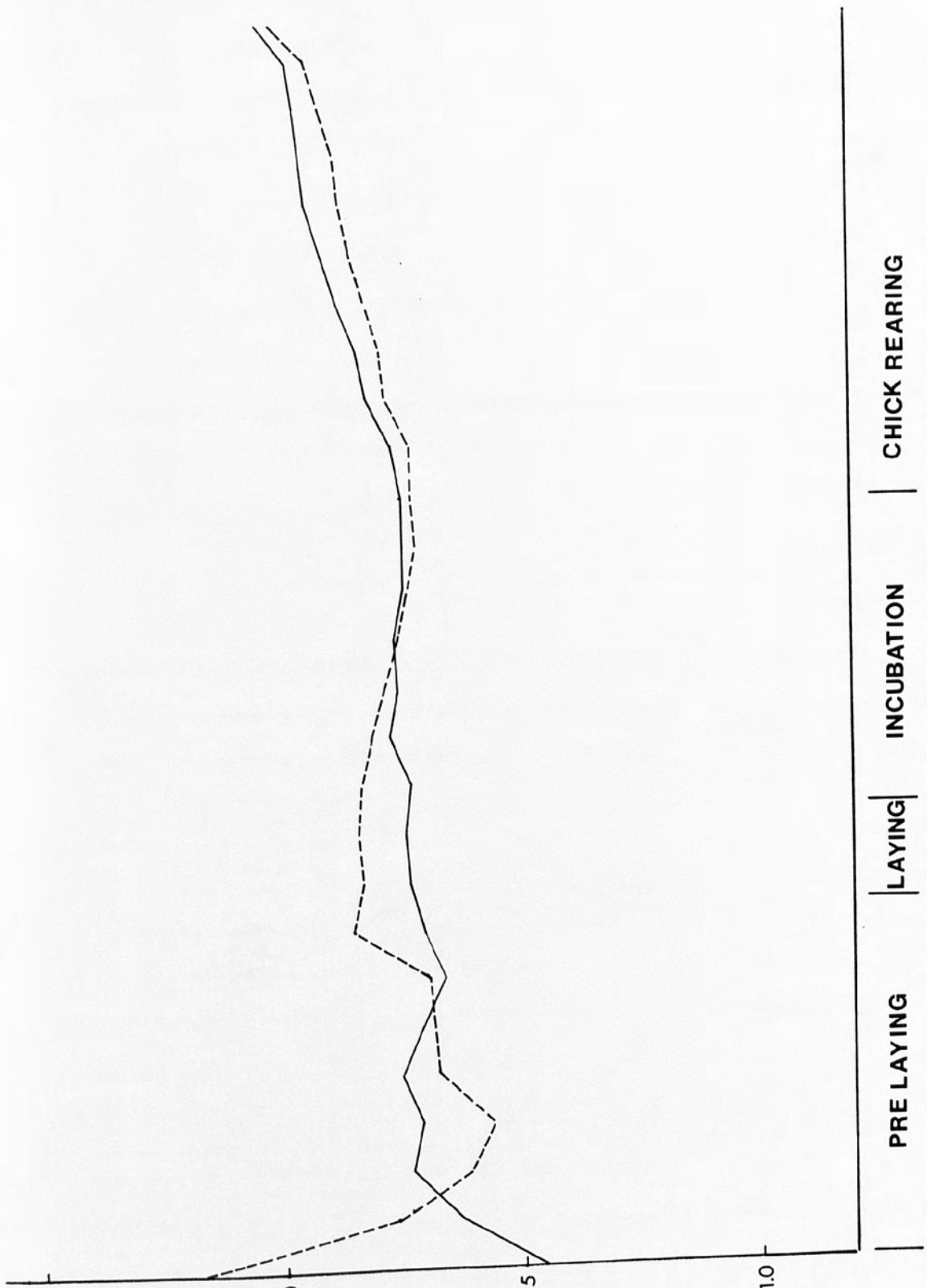
5%. Both sexes increase their rate of energy expenditure equally during the chick-rearing period over that during incubation, except during the last 10 days when chicks are very near to fledging (about 43 days). At this time the rate of energy expenditure of the female increases relative to that of the male and the final total energy expenditure of the female is slightly higher than that of the male (54,647 kcal vs 51,410 kcal). With respect to the percentage of cumulative daily BMR (Fig. 6), males in the pre-laying stage expended a larger multiple of their BMR than did females. The situation is reversed during laying and through the first 15 days of incubation, but thereafter both sexes expend about equal and steadily increasing multiples of their daily BMR's through to the period when chicks are present. At fledging, both parents are expending an average of two times their cumulative daily BMR to feed the chicks.

4. Discussion

A basic condition for the evolution of cooperative rather than adversarial interactions between parents is that the young cannot be raised successfully by one parent alone. The probability of finding another mate after deserting (e.g., Maynard Smith 1977) should only be an important factor in influencing a birds 'decision' to desert if there is a sufficient probability that the deserted mate can raise the offspring by itself. Otherwise the former decision becomes irrelevant.

Complementarity of parental abilities (Trivers 1972) should evolve when bi-parental care is necessary to successfully rear young. The sex

Fig. 6. Daily energy expenditure (kj) as a proportion of basal metabolic rate for male (solid line) and female American Oystercatchers (dashed line) over the breeding season.


DEE/BMR
2.5
2.0
1.5
1.0
PRE LAYING
LAYING
INCUBATION
CHICK REARING

with the choice of mate should choose a mate that not only provides genes that promote the survival of the offspring, but also provides parental care so the offspring are raised efficiently. In this study sex roles within pairs were very similar and overall energy expenditure similar for each sex. Where there was the potential for conflict in the pair in anti-predator behaviour, territorial behaviour and when feeding chicks, there was no evidence for such interaction.

However, complementarity should be the most evident during energetically costly periods in the breeding cycle. The high energetic demands of parenting in oystercatchers suggests that selection should act to favour behaviour patterns by the males which protects their paternity. An increase in chasing conspecifics by males during the late pre-laying and laying periods suggests that cuckoldry sometimes does occur. Although I never observed cuckoldry, the following observation was made in 1979 by A. J. Baker. Both members of one pair returned on schedule but only the female of a neighbouring pair returned. For 10 days the male of the first pair copulated both with its mate and with the lone female. The mate of the lone female then returned and the first male discontinued the extra-pair copulations. During the period when cuckoldry is likely to occur (during the late pre-laying and early laying periods) mates stay very close to each other and are usually in the same place. This also implies mate guarding. Are there males in the population who could possibly be a threat to paternity? During the pre-laying period in one year of the study (1982) seven mated males were removed from a stretch of beach adjacent to the main study area. In June of that year six of the females were still unmated, which suggests that there

were few excess males in the population, or if there were they chose not to pair with these unmated females. In July of each year it was common to observe single birds land on the territories of pairs of oystercatchers and engage in prolonged piping displays with the residents. These single birds, if males, were more likely scouting for a place in the subsequent years' breeding population than attempting to cuckold existent territory holders because of the improbability of beginning a clutch in July. Cuckoldry may be rare, but the costs of being cuckolded (particularly considering the high cost of parental care) are so great as to warrant the intensive precautions seen here.

Mate guarding by the female to reaffirm the pair bond is probably implicated in the observation that after a piping bout in the air during the pre-laying stage, the pair almost always copulated, with the female apparently initiating the copulation (pers. obs.).

During incubation, sex roles and energy expenditure by each sex diverge from that observed during pre-laying and laying, and at least a part of the difference in roles is accounted for by differences in the relative efficiencies with which each sex performs different tasks. Males spend more time watching for predators, and females spend more time incubating, and it costs females less per unit time to incubate. Selection should favour some form of bi-parental incubation if high losses of eggs due to predation or exposure occur when the nest is unattended. As well, selection should act against birds which overly exploited their partners during incubation if their partners are in correspondingly poorer condition for chick-rearing because of the exploitation (Niebuhr 1983). Only rarely did I see conflict at the nest over changeovers. Perhaps, as hypothesized for Herring Gulls (Larus

argentatus), the bird incubating may try to accommodate to the schedule of its mate (Niebuhr 1983) if this accommodation increases the probability of its mate surviving to the next breeding season (Coulson 1966, Mills 1973).

The evidence from this study suggests that males perform chases whenever the opportunity arises, even though they could at times leave it to their mates. During incubation there was no relationship between when a bird chased an intruder, and when its mate did, presumably due to the potentially high costs of leaving eggs uncovered. In piping behaviour, where the costs of leaving the eggs uncovered were not high (because intruders were other oystercatchers), the incubating bird left the nest and both members of the pair participated. This also indicates that the function of a territory in oystercatchers is not asymmetric, at least during incubation. Oystercatchers probably defend a nest site and hiding places for the chicks during territorial defense. The intensity, and presumably effectiveness of the piping display in maintaining a territory usually increased when both members participated.

Oystercatcher chicks, on hearing the alarm notes of their parents, flee to the nearest cover and crouch (Lind 1965), unless they are less than one week of age when they simply crouch in place. The most effective anti-predator behaviour for maintaining the safety of the brood early in chick-rearing, would be for one parent to stay near the brood if the predator strays too close, or otherwise participate in the anti-predator chases by the mate. Later in chick-rearing, the most effective behaviour would be for both parents to chase off or distract the potential predator. Standing near the site where the chicks last were might

increase the probability of discovery of the chicks by the predator. Hence, from the early to late periods of chick-rearing, the coordination of anti-predator behaviours between mates increased. The coordination of territorial defence between mates also increased, possibly reflecting the need for larger or more exclusive feeding areas with larger chicks.

The chick-rearing period (especially near the end), is the time when deserters in the pair bond are most likely to be observed. This is because the mate that continues with the parental duties has so much to lose if it does not continue (Trivers 1972), and the defaulter would likely get away with minimal fitness cost and would gain if it decreased its own probability of mortality. Defaulting by one parent at the end of this period is common in several monogamous shorebirds that do not have extensive parental care (e.g., Lapwing (Vanellus vanellus), Green Sandpiper (Tringa ochrops), Common Sandpiper (Actitis hypoleucos),(Bannerman 1961); Stilt Sandpiper (Micropalama himantopus)(Jehl 1973); Greenshank (Tringa nebularia) (Nethersole-Thompson 1951); Ruddy Turnstone (Arenaria interpres)(Nettleship 1973); Dunlin (Calidris alpina)(Soikkeli 1967); Killdeer (Charadrius vociferus)(Lenington and Mace 1975)). This phenomenon has been linked to food stress and declining weight of the deserter (usually female, Holmes 1966, Ashkenazie and Safriel 1980). Desertion by one mate is less common in short distance migrants (Lenington 1980) and this is probably because the energetic demands for migration are less severe.

There was no evidence from the results of this study that one or the other parent was defaulting or even contributing less than necessary in foraging for the young. Relative energy expenditure during this

period was high and steadily increasing over the chick-rearing period. Foraging trips were sometimes so frequent, that in all pairs observed the young rejected the food presented by the parents. Males waited longer before their next foraging trip than females, but the length of the wait did not seem to depend on which bird had made the previous trip.

Males spent only slightly more time at the foraging sites than females but took many more foraging trips. There was no indication that males and females foraged at different levels of efficiency. The longer periods of feeding by males may have been a result of the larger number of trips, because males may have required more food intake to compensate. How the parents divided their time on the foraging areas, between searching for food for themselves, and searching for food for the chicks, is not known. The trips by both sexes were usually of such short duration that the birds probably only had time to find one food item (usually bivalve mollusks) for themselves, and one to carry back to the young. Neither adult was ever observed carrying more than one food item. In H. ostralegus the parents bring food for chicks until they are satiated, then (and only then) do they forage for themselves (Norton-Griffiths 1969). Satiation of the young is indicated when the young no longer eat the food items presented to them (Norton-Griffiths 1969).

The sex roles in American Oystercatchers diverge during late chick-rearing when males perform more long piping bouts with intruding oystercatchers than do females. Females spend more time than males near the chicks. Females are still involved with territorial behaviour at this time but participate for shorter periods. Presumably the function

of the territory is still important to both sexes, but because the chicks are grown, the number of foraging trips decreases and the threat of predation is less. Therefore there is less need for both adults to spend all their time caring for the chicks. After the chicks fledged the male territory owner was often seen on the territory defending it vigorously from conspecifics while the chicks and females were away on the foraging areas. The female and chicks would usually return in the evenings. Defending the territory may have an important function in securing the territory for the next breeding season. It is late in the season when the threat from single 'floaters' appearing on the territory becomes most intense and it may be that this division of parental effort is again strictly following functional needs.

Cumulative energy expenditure (CEE) curves matched the generalized curves of Gladstone (1979) for colonial birds where extra-pair copulations have been observed. They indicate that CEE is equal in the sexes. Equal energy expenditure by each sex once the cost of flight by each sex was accounted for, was also found to be equal for the monogamous Northern Gannet (Sula bassanus) (Montevecchi et al. 1984). The only way 'parental investment' could be drastically different from what is depicted in the curves is if there was differential mortality between the sexes on the wintering grounds, in which case, the sex with a higher rate of mortality would be investing a larger proportion of his or her residual reproductive value (Williams 1966) to this years reproductive effort (assuming mates are of the same age, and begin breeding at the same age). If the rate of annual return to the nest site is assumed to be a measure of the survival rate and not a measure of the dispersal rate, then it appears that both sexes of the American Oystercatcher have

nearly identical mortality rates (= 1 - survival rate) (males, 84.4% mean annual return; females, 84.6% mean annual return, n = 5 years).

Complementarity of mates should be enhanced when the probability of maintaining the same pair bond in future breeding attempts is high (Trivers 1972, Niebuhr 1983), or the probability of finding a new mate of comparable or better quality is low. Cooperative behaviour should be found most often in long-lived species with stable pair bonds. Earlier, however, I stated that the one pre-condition for the evolution of cooperative behaviour was a difference between the probability of raising chicks alone, and the probability of raising chicks with a mate. Complementarity, and the need for extensive bi-parental care probably evolved together, along with stable pair bonds and longevity. It may be, as Knowlton (1979) suggested, that extensive parental care by the male evolved in response to increasing reproductive synchrony on the part of the female. Once extensive male parental care was in place, it became difficult for males to obtain new mates from one season to the next, and it 'paid' both parents to act cooperatively.

A mechanism is likely to have evolved whereby a parent can assess the incompetence of its mate, and either divorce the mate early in the breeding cycle, or raise chicks with an incompetent mate. M. D. Cadman (pers. comm.) has observed one divorce in oystercatchers after loss of the first clutch of eggs to predators, and the altercation between the mates appeared to be initiated by the male. Incompetence was observed in one parent that 'presented' food repeatedly to a newly hatched chick from over 100 m away, out of view of the chick. Unfortunately this pair was unmarked and the fate of the pair bond is unknown. Presumably if one

of the parents is incompetent then the other will seek a new mate at the beginning of the next breeding season.

Chapter 4: ENVIRONMENTAL PREDICTABILITY AND LIFE-HISTORY TRAITS OF OYSTERCATCHERS

1. Introduction

The study of life history evolution has amassed evidence supporting the existence of two alternate sets of life-history traits (Pianka 1970, Gadgil and Solbrig 1972, Abrahamson and Gadgil 1973, Gaines et al. 1974, Menge 1974, Richardson 1975, Law et al. 1977, Stubbs 1978, Tamarin 1978, Leutonegger 1979, Barclay and Gregory 1981, Stearns 1983a, Allan 1984, Stearns 1984). One set includes slow development and late maturity, small reproductive effort, fewer young and long life. The other set includes rapid development, early maturity, large reproductive effort, more young, and short life (Pianka 1970). These two alternate sets of purportedly coadapted traits, or life-history tactics (Stearns 1976), appear to be associated with a single ecological dimension: environmental predictability. Fluctuating and stable environments can influence adult or juvenile mortality or both. The stage at which the level of predictability acts is crucial in understanding the consequences to the life-history traits (Stearns 1976, Charlesworth 1980, Stearns 1983b). Unpredictable mortality rates for the adults select for increased reproduction early in life. High, variable or unpredictable juvenile mortality rates, with stable adult mortality, select for decreased annual reproduction and longer reproductive life (Stearns 1983b). Experimental

tests of these specific predictions are rare, both in vertebrates and invertebrates (Parry 1981) and most work has been comparative (Richardson 1975, Schwartz 1984, Stearns 1983a,b, 1984).

In birds, different levels of environmental predictability may explain variability in clutch size (Williams 1966). This hypothesis predicts that two closely related species living in equally stable environments for the adults (and with equally variable juvenile mortality) should have the same clutch size. Species living in unpredictable environments for the adults should have higher clutch sizes than species living in stable environments. By contrast, Lack (1968) suggested that the clutch size of birds that feed their young was adjusted to the average amount of food available for feeding the young. In a within species comparison this hypothesis is supported if large clutches are laid by females with more food available during chick-rearing. The same prediction should apply when comparing related species. Females of species having greater access to food for the young should lay larger clutches. For several species of larids, all of which feed their young, it has been suggested that clutch size may also be influenced by the amount of food available to the laying female (Larus argentatus, Parsons 1975; Sterna paradisaea, Coulson and Horobin 1976; Larus novaehollandiae, Mills 1979). This hypothesis is also considered here for explaining clutch size variation in oystercatchers and can be rejected in a within-species comparison if the quality of the territory as a place to acquire food during pre-laying is not positively correlated with the size of the clutch.

Here I compare life-history traits of H. palliatus palliatus, the American Oystercatcher, in Virginia with H. ater, the Blackish Oystercatcher, in southern Argentina. I compare both species with H. p. durnfordi in Argentina where it is sympatric with H. ater. The three taxa differ in their mean and modal clutch sizes. I test Lack's hypothesis by comparing time budgets of H. p. palliatus in Virginia with those of H. ater in Argentina. I then test whether food limitations in the prelaying period are correlated with clutch size in H. p. palliatus by computing correlations between territory quality and several reproductive performance parameters.

Without data on age-specific mortality rates I do not directly test the above predictions of life-history theory. I ask two questions: (1) Can the differences in environmental predictability that we perceive between two sites be translated into differences in environmental predictability from the perspective of the birds, and (2) Can the differences in life-history traits among the three groups of oystercatchers be explained by differences in environmental predictability?

This chapter is organized as outlined below. To test the direct effect of differences in food availability to clutch size variability (e.g., Lack 1968) I measure time budgets and feeding efficiency of H. p. palliatus in Virginia and H. ater in Argentina. Environmental predictability may affect life-history traits because predictable environments may result in the extension of the reproductive life of the organism. I ascertain predictability with regard to the following factors in both species of oystercatchers: feeding behaviour, behavioural diversity, egg-size variability, habitat variability and climatic stability.

2. Methods

The study was conducted on H. p. palliatus in coastal Virginia (see Chapters 2 and 3 for details of study area) during the breeding seasons of 1981 to 1983, and H. ater and H. p. durnfordi at Punta Tombo, Argentina (44° 02'S, 65° 12'W) during two weeks in November, 1981 and November and December 1982. Punta Tombo consists of volcanic rock outcrops interspersed with sandy beaches and rocky intertidal areas.

2.1. Study Animals

Most individuals in the study population of H. p. palliatus were marked with plastic colour bands and U.S.F.W.S. bands. Individuals of H. p. durnfordi and H. ater were not marked and I made the assumption that birds in the same area from day to day were the same individuals. Observations on the marked birds in Virginia suggested that this was a realistic assumption. I sexed H. p. durnfordi and H. ater by observing differences in bill length, bill coloration, back colour and copulatory position. Males of both species have shorter bills of a deeper red than do females, and in H. p. durnfordi, the males have slightly darker brown backs than females (Miller and Baker 1980). H. ater is larger than either H. p. palliatus or H. p. durnfordi, and has a slightly shorter bill and legs (Baker unpublished data).

2.2. Daily time budgets

Time budgets were examined to test the specific hypothesis that food shortages in the pre-laying period and/or chick-rearing periods could explain the differences in clutch size between the two species. To construct time-budgets observational data were collected during continuous-observation focal-animal sampling sessions of 10 min each (Altmann 1974). These samples were collected within 4 to 6 hour blocks of time for H. ater and H. p. palliatus during the pre-laying period. For H. p. palliatus during chick-rearing, sampling sessions were longer (up to 12 h, see Chapter 3). I collected these data with an electronic event decoder (International Instruments Inc.), which provided an accurate time base (± 0.1 sec) for activities, and accurate counts of frequency of those activities which I considered had too short a duration. These data were supplemented with time-budget data recorded manually, or on a hand-held dictaphone, and these durations were accurate to about ± 2 sec.

Individuals to be sampled during these periods were chosen randomly, but the periods were chosen systematically with respect to the time of the day (see Chapter 3). The result of this sampling scheme was an unequal number of samples on each bird, but each bird was sampled approximately evenly throughout the day and with respect to the phase of the tide.

I recorded 57 behaviours which I categorized into the same 22 categories as in Chapter 3. In addition I also recorded the length of flights to and from the feeding areas, the amount of time on the feeding

area and the total amount of time on the nesting area. These latter variables, along with the information on the food available on the territory, were used in the analysis of territory quality (see below).

2.3. Feeding behaviour

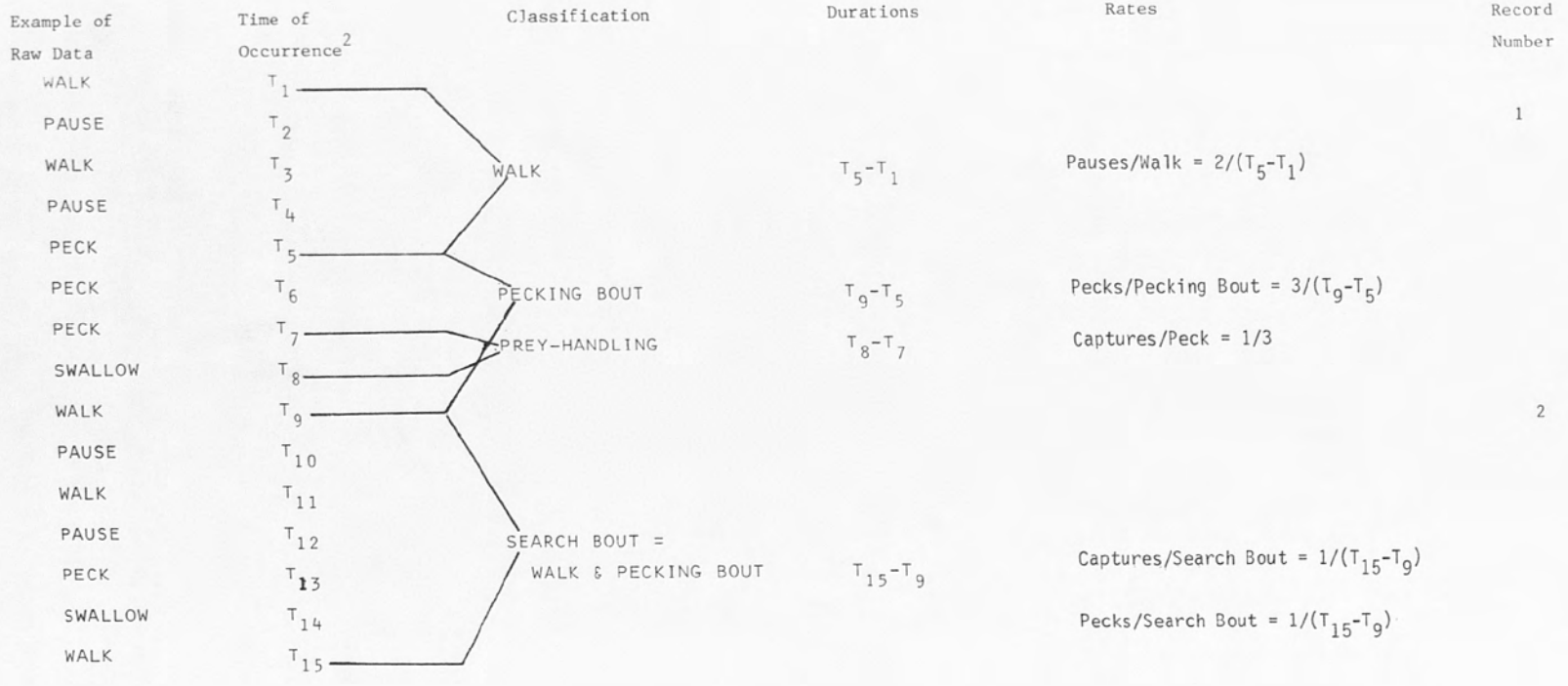
I used the electronic event decoder in conjunction with written notes to collect continuous records of the foraging behaviour of a total of 86 individuals of H. p. palliatus, H. p. durnfordi and H. ater. The records included prey type, prey size with respect to the birds' bill length (both recorded by hand), length of walk, number of pauses in walk, number of pecks in a pecking bout, the number of pecks ending in capture of a prey item, handling time (Fig. 1), step rate, and the zone the bird was feeding in (see description of habitats below).

Once an individual stopped searching for food I switched to another to allow sampling of as many individuals as possible. This resulted in never sampling the same individual twice. I only sampled pairs in which the female had not yet laid any eggs (i.e., both birds in the pair were on the feeding areas together).

Feeding and nesting areas in Virginia were usually separated by 100 to 1000 m (Fig. 2), and the former were usually not visible from the latter. In Virginia, I recorded feeding behaviour of oystercatchers on large mudflats around islands, or in the channels of the salt marsh, except for those individuals that had feeding areas adjacent to their nesting areas. In Argentina the birds of both species flew or walked to the intertidal areas immediately adjacent to their nesting areas and I

Fig. 1. Structure of foraging data collected with event decoder.

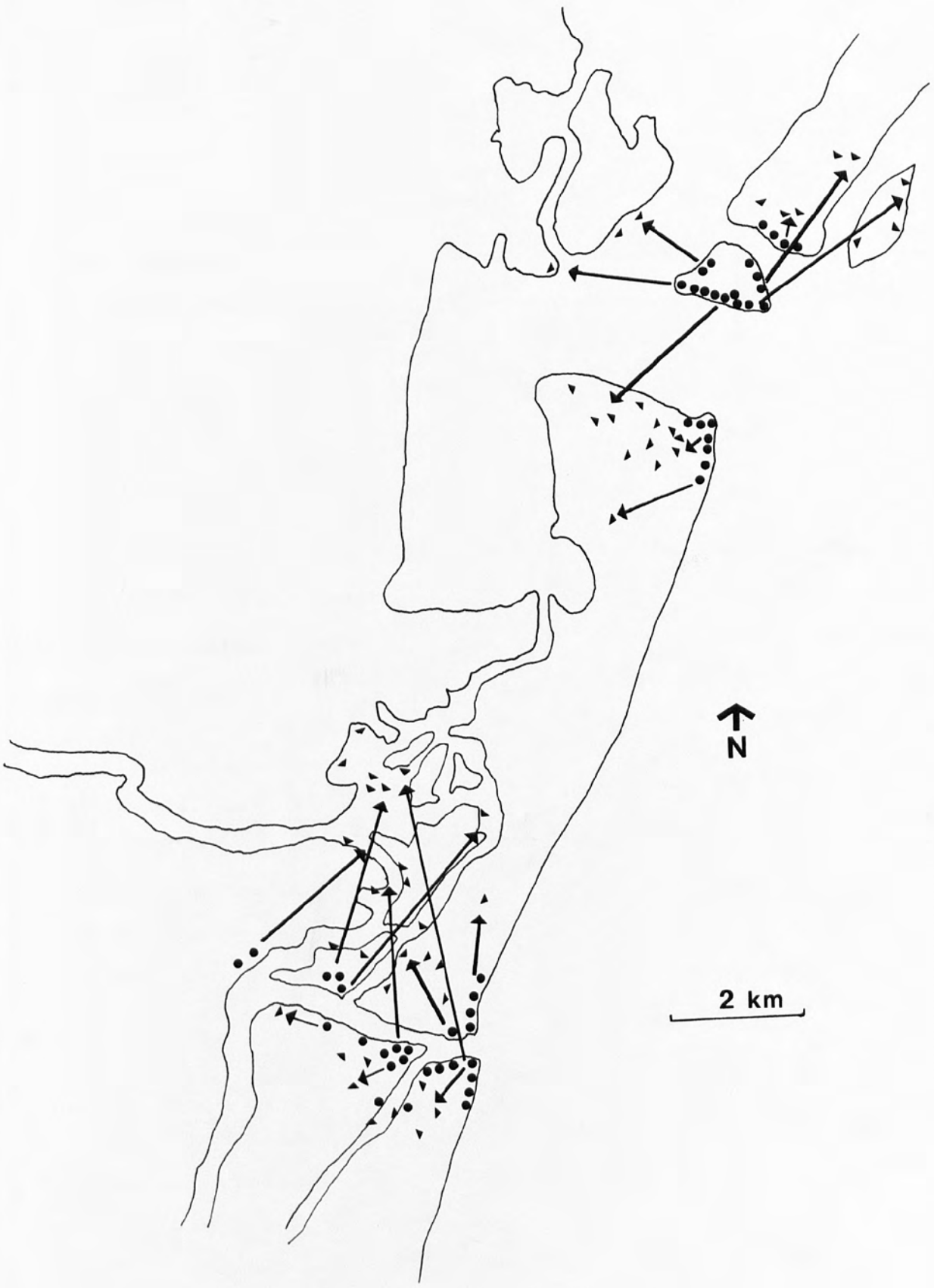
Figure 1. Structure of foraging data.[1]



[1] The entire observation period on one individual constitutes a foraging bout.

[2] From raw data.

Fig. 2. Spatial relationships of feeding (triangles) and nesting (circles) areas of H. p. palliatus in the Virginia study site. Arrows indicate general relationships between groups of nests and the feeding areas.

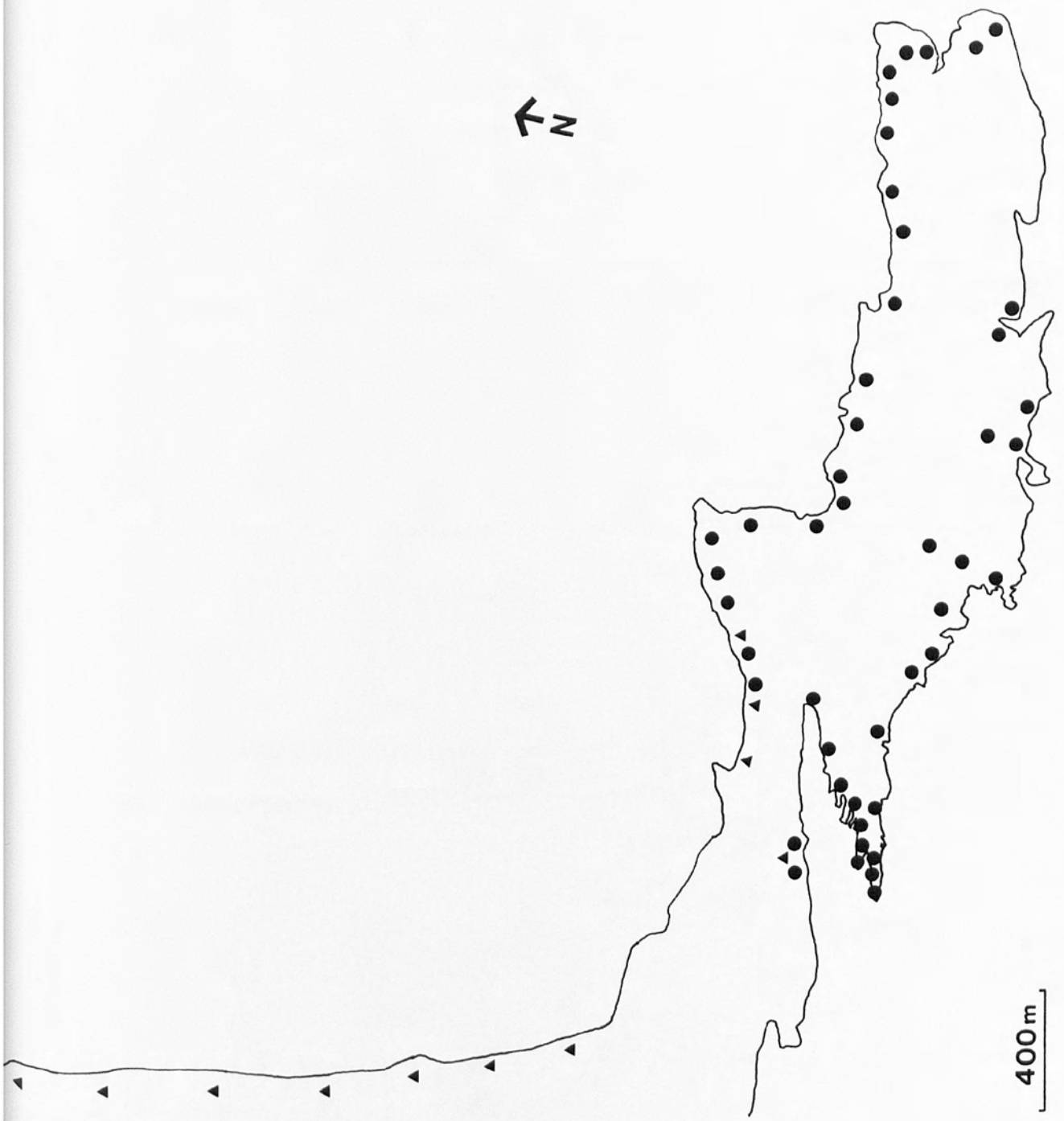

N
2 km

recorded the feeding behaviour there (Fig. 3).

2.4. Feeding path analysis

In addition to recording lengths of walks and pecking bouts I was also interested in whether the pattern in which the bird moved through the feeding areas reflected the relative patchiness or homogeneity of the prey. I observed feeding birds, and in a notebook, I drew the path the bird was following through the habitat, with some stakes and natural landmarks to indicate scale and where the bird was at any given time. I attempted to move my pencil at a constant speed relative to the speed at which the bird traveled so that distances within a path were accurate relative to the full length of the path. I used the full length of the path to standardize the distances of segments of the path among birds. The zones (see below) in which the birds were feeding were also recorded. As with the foraging data, I tried to obtain paths on as many individuals as possible, foregoing the acquisition of replicates. In both the foraging and feeding path analyses this was necessitated by not being certain of which individuals of H. ater I was observing. I took care to move to new areas each time I recorded paths or foraging bouts so to avoid sampling the same individual more than once. If this was done inadvertently, the effect on the results (i.e., some lack of independence) is probably minor due to the fairly large sample sizes. I applied the same sampling techniques to H. p. palliatus to standardize results. Too few paths were obtained on H. p. durnfordi to include in the analysis.

Fig. 3. Map showing locations of pairs of H. ater (circles) and H. p. durnfordi (triangles) on Punta Tombo, Argentina.


N
400m

2.5. Egg parameters

In both study areas I monitored nests from pre-laying through to the chick-rearing periods, to determine egg-size ordering, clutch size, clutch-initiation dates, and hatching success (see Chapter 1). Actual visits to the nests were confined to the laying period. The incidence of predation after the laying period, and the presence of chicks was determined by observing the nest site and the incubating adult through binoculars, from a distance as far as possible from the nest to minimize the effects of disturbance on reproductive success.

2.6. Behavioural diversity

On 12 days I conducted lengthy observations (4.5 to 12 h) on 6 to 24 individuals of oystercatchers to establish how the level of the tide affected the movements of the local population of birds. Specifically, I was interested in whether all birds moved synchronously to the inter-tidal zones, or whether their behaviour was staggered and unpredictable. I used a scan sampling technique (Altmann 1974), and every 10 min recorded the behaviour and location of all individuals visible. If individuals of H. p. palliatus were off the nesting area I assumed the birds were on the feeding areas.

2.7. Habitat sampling

2.7.1. Habitats used by H. p. palliatus

American Oystercatchers feed in a variety of habitats and on a variety of prey items in the breeding season. I observed birds feeding on the large, open tidally exposed mudflats, where they hunted primarily for common razor clams (Ensis directus) and little green razor clams (Solen viridis) (zones 1E, 1S). In small (< 0.5 ha) clearings in the salt marsh, and along the channels and tidally exposed bars they fed on ribbed mussels (Modiolis demissus)(zone 1M), and on small muddy bars along the channels they fed on stout tagelus (Tagelus plebeius) (zone 1T) or Solen viridis. The oystercatchers also fed occasionally in the ocean surf on mole crabs (Emerita talpoida) and on the commercial oyster beds of Crassostrea virginica (zone 10).

To assess the distribution of prey, I chose six representative feeding areas and set up plots of between 1200 and 2400 m^2 (depending on the habitat) with stakes indicating every 5 to 10 m. At each stake I laid down a 1 m^2 quadrat frame and counted all bivalves, percent cover of salt marsh grass (usually Spartina sp.) and percent open ground.

The abundance of organisms available as prey on the different nesting territories was measured by quadrat samples at 30 territories. The locations of the samples were chosen randomly within the feeding areas. The number of samples varied from 15 to 35, depending on the total size of the feeding areas. These data were used as a measure of richness of

the feeding areas on the individual territories and used in the measurement of territory quality (see below). The size of the area containing food was also measured, using the pace and compass technique.

Oystercatchers leave the shells of molluscan prey at the feeding areas. The size distribution of prey was determined by collecting all shells at four mussel areas, two areas containing Tagelus, one area containing Solen, and two areas containing Ensis, and measuring their lengths. The relationship between wet weight and length of Modiolis, Tagelus, Solen, and Ensis was determined by weighing a sample of live animals without the shells, to the nearest ±0.1 g. I used the wet weight/ length relationships to calculate the frequency distributions of biomass of the shells left by the birds. The relationship between length and volume of these bivalves was determined by measuring the volume of water displaced by the live animals. The relationship between wet weight and volume was about 1:1. This relationship was used below in determining the wet weight of the prey from Argentina, for which I had no actual wet weights.

2.7.2. Habitats used by H. p. durnfordi and H. ater

The two species living in Argentina fed on the rocky inter-tidal areas that were exposed only when the tide ebbed. On the ebb tide the oystercatchers moved toward the low water mark. The prey items available varied as a function of the distance from the high water mark. All birds observed fed in this inter-tidal area.

Six zones, including the nesting areas, were identified from the rocky and sandy dry areas of Punta Tombo to the low water line. These were: (1) rocks and sand never exposed to the tidal spray during the breeding season (zone 1), (2) spray zone; sandy areas sprayed only during severe winds (zone 2), (3) high tide zone, characterized by scattered small Modiolis (10-80% of rocks covered), small tidal pools and bare rock (zone 3), (4) mid-tide zone, 50% to 100% cover of Modiolis of size class < 1.8 cm, and small patches of bare rock (zone 4), (5) mid- to low-tide zone, 50 % to 100 % cover of Modiolis of size class 1.8-2.5 cm,(zone 5),and (6) laminarian zone with scattered large (> 2.5 cm) mussels (Mytilus) and limpets (Acmea, zone 6). Zones 4, 5 and 6 were categorized as to whether the birds were feeding on limpets (zones 4L, 5L, and 6L) or mussels (4M, 5M, and 6M).

To assess the changes in distribution and abundance of prey along the line from high water to low water, I sampled five transect lines (three on H. ater territories and two on H. p. durnfordi territories), with 50 X 50 cm quadrats laid down at 5 m intervals. I counted (or estimated) the number of mussels and limpets, and the percent of the area in the quadrat covered by mussels, rock, water, laminarian algae,

and sea lettuce. The size distribution of prey was determined by collecting a sample of 20 prey items at each quadrat along the transect lines and measuring each individual. The biomass of mussels was determined by calculating the volume of prey as (length X breadth X 0.25 width)/1000, and converting directly to wet weight. The volume of limpets under 20 mm was calculated by the formula: log (wet weight) = 2.77 x log (length) -4.33, and over 20 mm, by the formula: log (wet weight) = 5.86 x log(length) -8.31 (Groves 1982).

Patchiness of the habitat and how well the distribution of prey in one transect could be predicted by the distribution of prey in an adjacent transect was assessed by setting up three plots of varying sizes from 20 X 35 m to 20 X 65 m (depending on the size of the inter-tidal zone) containing four transect lines 5 m apart. At each 5 m I laid down a 50 x 50 cm quadrat and recorded the same information as recorded in the transect lines.

2.8. Territory quality and reproductive performance

Three parameters were used as measures of territory quality. These were size of the feeding area within the nesting territory, distance from the nesting area to the regular feeding area, and density of food on the nesting territory. These three were chosen because they related to the quality of the territory in providing food for the territory holder during pre-laying. Average egg-size, size of first clutch, size of second clutch, clutch initiation date, interval between loss of first clutch and laying of replacement clutch, and an index of the stability

of the pair bond (no change of mate in years under observation - 3, one change - 2, greater than one change - 1) were used as measures of reproductive performance.

2.9. Statistical analysis

All time budget data were tested for normality with the Kolmogorov D test (Sokal and Rohlf 1981) and then transformed, if not normal with an arcsin transformation (duration data) or the square-root transformation (frequency data). Univariate non-parametric and parametric analysis of variance were used to test for differences between species and sexes in the allocation of time to different activities in the pre-laying period. Since there existed a high degree of interaction among the time-budget variables (e.g., if the bird was feeding it could not sit), I also compared between species and sexes with a multivariate analysis of variance on transformed data, and canonical discriminant analysis. My objective was to look for interactions among variables, and to test for differences among groups, using all variables simultaneously (Cooley and Lohnes 1971). Canonical correlation analysis was used to examine the linear relationship between territory quality and reproductive performance (Tatsuoka 1971).

If life-history traits are influenced by the predictability of the environment then the proximate effects of that predictability should be manifest in the diversity of the behavioural repertoire of the organism in the environment. A population of organisms inhabiting very simple predictable environments should show less behavioural diversity than a

population inhabiting a more complex, or unpredictable environment. I calculated the Shannon-Weaver index (H) of diversity of behavioural acts exhibited in each 10-min scan sampling period (Pielou 1975), through one full tide cycle. For each species, I plotted the H values against time from low tide and compared the results visually.

For H. ater, I was able to observe, through the full tide cycle, the exact location of each bird at each 10-min scan. The average zone occupied by all birds over the tide cycle was computed and fitted to a harmonic regression to assess the predictability of the birds movement through time. The data for two separate days of observations were linked to provide a record of two tidal cycles.

In the analysis of feeding behaviour the sequences of various characteristics of searches, turns, etc. that the bird made during a foraging session were examined. I tested for non-randomness of these sequences with the runs test (Sokal and Rohlf 1981). Directionality in the paths was tested using Raos' test (Batschelet 1981). Comparison between variability of variables was tested by applying the log transformation to the coefficients of variation (as recommended by Bader and Lehmann 1965), and comparing the transformed coefficients of each pair of species (e.g., H. p. durnfordi with H. p. palliatus, H. p. palliatus with H. ater, H. p. durnfordi with H. ater) with an F-test (Sokal and Rohlf 1981).

2.10. Predictability of environment

In addition to assessing the predictability of the environment using the behaviour of the birds and the pattern of prey distribution, I also used a standard measure (ΔT) of seasonality (MacArthur 1975), the difference between mean temperatures in January and July. Colwell (1974) suggested that not only should seasonality be measured, but also contingency, the regularity of the seasonal fluctuations from year to year. I ascertained contingency by computing the standard deviations in monthly and yearly temperatures over a 20-year period (1963-1982). These were compared between the two study areas and tested for significance with a t-test. Weather information was obtained from the World Climatology Surveys of the National Oceanic and Atmospheric Administration reports.

The environmental predictability hypothesis implies that selection, through differential adult mortality patterns affects not only clutch size but other life-history attributes like body size, migratoriness and nesting densities. The patterns of migration of H. p. palliatus, H. p. durnfordi and H. ater were obtained from the literature, as well as all other ecological data on the other species of oystercatchers. Weights of H. ater and H. p. durnfordi were obtained from birds collected in southern Argentina by A. J. Baker in 1977 and 1981. Growth parameters for the chicks of H. p. palliatus were obtained by capturing and measuring as many known-age chicks as possible, over the three years of the study.

3. Results

3.1. Clutch sizes

Both species of Haematopus in Argentina lay a modal clutch of two eggs (Table 1). H. p. palliatus in Virginia lays a modal clutch of three in the first nesting attempt and a modal clutch of two eggs in repeat attempts (Table 1).

3.2. Lack's hypothesis (food limitation during chick-rearing)

3.2.1. Time budgets

Birds of both species were observed for a total of 435 h during the pre-laying period: some of these hours were spent in 10-min continuous sampling periods, and some in scan-sampling sessions (Table 2). H. p. palliatus in Virginia was also observed for over 400 h during the chick-rearing period (Table 2). During the study period only one pair of H. ater in Argentina raised a single young. Therefore, for the comparison of food available to each species during chick-rearing I make the assumption that the oystercatchers in Argentina are feeding as much in the pre-laying period as they do during chick-rearing. The assumption is probably correct because the birds in Argentina feed steadily throughout the period when food is uncovered by the tide and therefore

TABLE 1. Frequencies of clutch sizes of *Haematopus p. palliatus*, in Virginia, and *H. p. durnfordi* and *H. ater* in Punta Tombo, Argentina.

	Mean	Number of eggs in first clutch					Number of eggs in second clutch				Number of eggs in unknown clutch				
Species		n	1	2	3	4	u[1]	1	2	3	u	1	2	3	u
H. p. palliatus	2.62	224	2	25	101	1	25	3	37	22	8				
H. p. durnfordi	2.31	22	0	15	7		5								
H. ater	1.91	41	1	25	0		2	2	2	0	0	1	6	0	2

1 u indicates clutches with an unknown number of eggs.

TABLE 2. Sampling effort by sex, species and sampling technique during the pre-laying period (for H. p. palliatus and H. ater) and during chick-rearing (for H. p. palliatus, see text).

Sampling technique	Species	Sex	Number of birds	Number of 10 min samples	Mean time per bird (h)	Total number of hours
10-min focal animal samples	Haematopus ater (pre-laying)	F	25	342	2.3	57
		M	22	292	2.2	49
	H. p. palliatus (pre-laying)	F	26	402	2.5	67
		M	27	384	2.2	64
	H. p. palliatus (chick-rearing)	F	19	-	22.1	421
		M	23	-	19.3	445
Scan samples	H. ater	F	12	-	10.9	33
		M	12	-	10.9	33
	H. p. palliatus	F	21	-	4.9	66
		M	21	-	4.9	66

available (see Results, Behavioural diversity below).

During chick-rearing the birds in Virginia increase the amount of time spent feeding by from 15.7% to 24.7% for females and 12.7% to 23.2% for males, but in neither period did H. p. palliatus spend as much time feeding as H. ater (Table 3).

3.2.2. Feeding efficiency

H. ater spends over twice as much time as on the feeding areas as does H. p. palliatus during the pre-laying period, and just less than twice as much during chick-rearing. Frequency distributions of the lengths and biomass of the food items available to H. ater and H. p. palliatus are given in Fig. 4. It is clear that the biomass of almost all the food items available to H. ater (items A. and B.) is lower than the biomass of food available and eaten by H. p. palliatus (items C,D,E, and F). The biomass of one average Modiolis available to H. p. palliatus is seven times that of the biomass of an average Modiolis sp available to H. ater (6.17 g vs. 0.85 g).

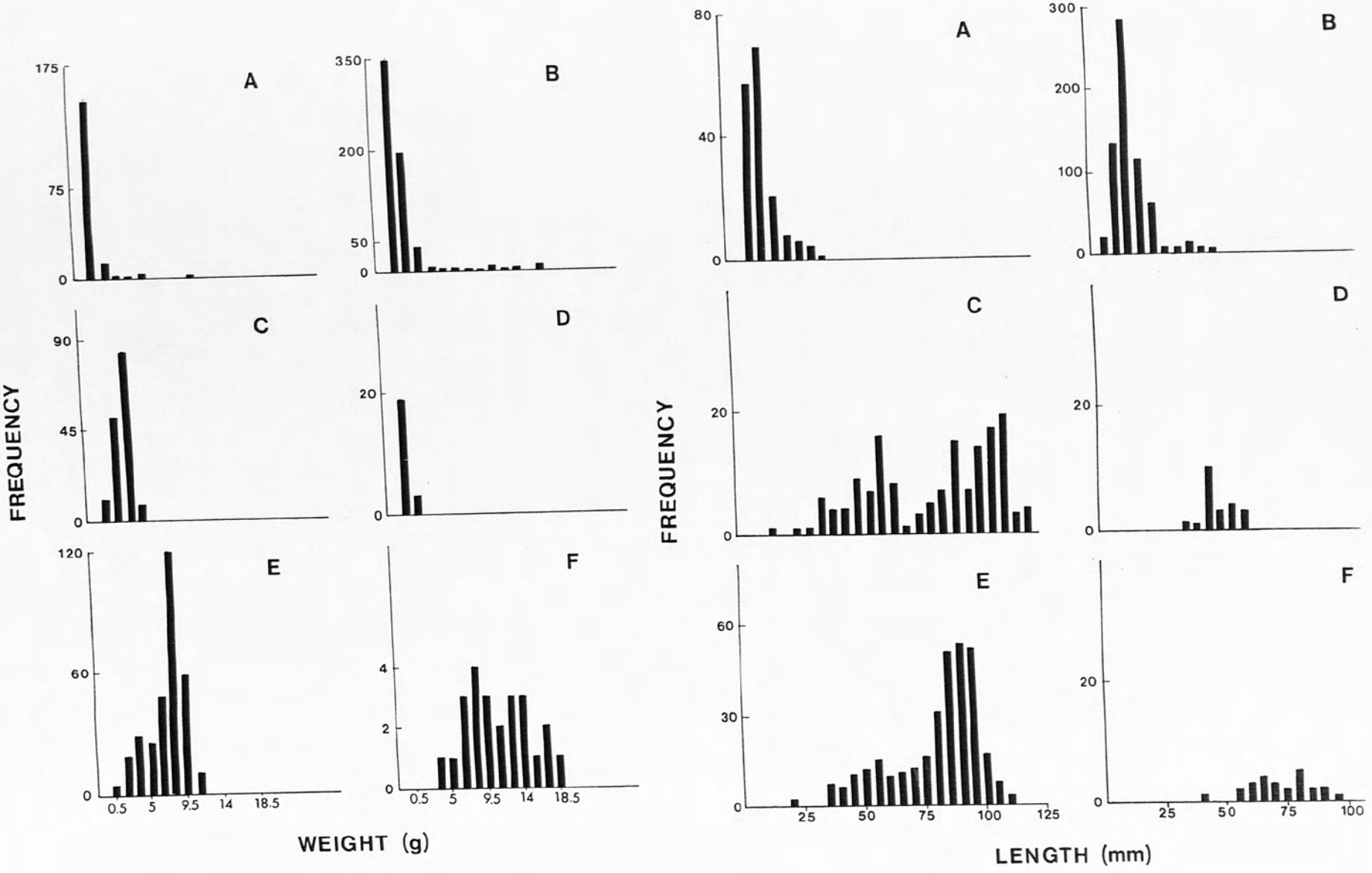
The number of successful captures per unit search time is 24.0/10 min for H. ater and 4.2/10 min for H. p. palliatus, (based on values from the pre-laying period) when the data from all feeding zones are combined. The lower rate of prey capture by H. p. palliatus is in part a function of the longer handling time per item for this species, but also depends on the distribution of prey. Handling times for all food items except Tagelus eaten by H. p. palliatus, were longer than handling times for items eaten by H. ater (Tables 4 and 5). The spatial

TABLE 3. Percent composition of activities and mean Kruskal-Wallis rank scores in the time budgets of H. p. palliatus during pre-laying and chick-rearing, and H. ater during pre-laying.

Activity code	H. p. palliatus Pre-laying ♀ %	H. p. palliatus Pre-laying ♂ %	H. p. palliatus Chick-rearing ♀ %	H. p. palliatus Chick-rearing ♂ %	H. ater Pre-laying ♀ %	H. ater Pre-laying ♂ %
Resting	27.10	27.96	2.8	2.8	25.16	29.97
Preening	9.95	11.47	3.9	2.7	1.75	2.64
Standing	25.72	25.14	37.4	31.4	10.36	10.47
Walking	7.29	7.32	5.3	5.9	1.89	3.88
Searching for food	15.7	12.7	24.7	23.2	39.92	34.48
Piping	1.00	0.68	2.2	2.6	0.44	0.61
Sitting	9.59	10.47	4.7	6.9	15.73	11.29
Bathing	0.31	0.28	0.05	0.3	0.03	0.06
Brooding	2.05	2.09	7.9	3.1	1.71	2.72
Flying	1.81	1.33	0.65	0.8	0.25	0.18
Crouching	0.21	0.25	0.45	0.23	0.30	0.92
No. of piping	0.07	0.06	0.064	0.081	0.04	0.05
Bobbing	0.24	0.18	0.029	0.044	0.01	0.02
Shaking	0.15	0.17	0.029	0.025	0.04	0.04
Chase others	0.003	0.01	0.0097	0.010	0.003	0.003
Chase oystercatchers	0.002	0.00	0.0068	0.018	0.002	0.002
Chased by oystercatchers	0.000	0.00	0.0057	0.014	0.006	0.005

[1] Searching for food is significantly different among three groups but not between sexes ($P < 0.0001$, Kruskal-Wallis rank test).

Fig. 4. Frequency distributions of the lengths (a) and biomass (b) of food items available to H. ater and H. p. palliatus. Items are Acmea (A), Mytilus (B), (eaten by H. ater), and Ensis (C), Solen (D), Modiolis (E), and Tagelus (F) (eaten by H. p. palliatus).


A
B
C
D
E
F
FREQUENCY
WEIGHT (g)
LENGTH (mm)
0.5
5
9.5
14
18.5
25
50
75
100
125

distribution of prey available to the two species of oystercatchers is very different. H. ater and H. p. durnfordi move from zone 4 to zone 6 as the tide recedes. The capture rate is dependent on the zone the bird occupies and the species of prey the bird is searching for (Table 4). The rate declines significantly near the low tide line (zone 6) where the bird searches for and takes the larger mussels and limpets (i.e., those sizes that fall in the tail of the distribution in Fig. 5). The average rate of food capture over the time available for feeding depends also on how long the bird spends in each zone. The total biomass consumed per daylight hours can be calculated from the formula:

$$\text{Total biomass} = p \sum_{i=1} x_i y_i z_i$$

where x=capture rate in items/sec

y=proportion of time in zone i

z=biomass/item captured in zone i

p=number of seconds spent feeding in a day

From this equation the calculated daily intake of the three taxa during pre-laying is as follows: H. ater, 583 g/day; H. p. durnfordi, 413 g/day; H. p. palliatus, 343 g/day. Expressed as percentages of mean adult body weight, by sex, these values are: H. ater, males 0.86, females 0.79; H. p. durnfordi, males 0. 85, females 0.68; H. p. palliatus, males 0.58, females 0.54. Both H. p. durnfordi and H. ater have a higher daily intake during pre-laying than does H. p. palliatus. The caloric values of the prey of each species are approximately equal (18.0 kj / g wet weight, Baker 1974).

TABLE 4. Comparative foraging data for H. ater and H. p. durnfordi when feeding on limpets or mussels.*

		H. ater		H. p. durnfordi	
Variable	Zone	Limpets	Mussels	Limpets	Mussels
Walk (sec)	4	1.95[1]	5.97	3.48[2]	6.92[a]
	5	8.11	5.37	10.92	4.55[a]
	6	-	4.95[1]	4.24	5.33[2,a]
Pauses/ Walk	4	1.63	0.65[a]	0.89	0.70[a]
	5	0.66	0.94[a]	0.71	0.73[a]
	6	-	0.98[a]	0.90	0.75[a]
Pecking bout (sec)	4	3.49	5.84[1]	3.83[a]	4.60[2]
	5	4.33	4.48	3.72[a]	3.89
	6	-	4.20	6.87[a]	3.46
Pecks/ pecking bout	4	1.37[1]	0.44	0.47[2]	0.56
	5	0.60[1]	0.74	0.71[2]	0.53
	6	-	1.05	0.43	0.91
Search bout (sec)	4	4.77[1]	11.71	7.31[2,a]	11.52
	5	12.44	9.85	14.64[a]	8.44
	6	-	9.16[1]	11.11[a]	8.79[2]
Pecks/search bout	4	0.66[1]	0.14	0.18[2,a]	0.15
	5	0.14[1]	0.31	0.19[2,a]	0.18
	6	-	0.39[1]	0.22[a]	0.21[2]
Captures/peck	4	0.254[1]	0.594	0.533[2]	0.566
	5	0.402[1]	0.273[1]	0.086[2]	0.420[2]
	6	-	0.144[1]	0.105	0.235[2]
Captures/search bout	4	0.10[1,a]	0.06	0.08[2]	0.06
	5	0.04[1,a]	0.05	0.01[2]	0.05
	6	-	0.02[1]	0.01	0.03[2]
Handling time (sec)	4	2.23[a]	2.00[a]	1.21	1.43[a]
	5	1.19[a]	1.82[1,a]	1.75	1.13[2,a]
	6	-	2.04[1,a]	5.87	1.40[2,a]

* Numbered superscripts indicate differences in attribute between species within the feeding zone and prey item. Lettered superscripts indicate homogeneous groupings within a prey item among feeding zones.

TABLE 5. Comparative foraging data for four different prey species taken by *H. p. palliatus* in Virginia.

Variable	Prey Item*			
	Modiolis (n = 175)	Crassostrea (n = 288)	Tagelus (n = 452)	Ensis (n = 574)
Walk (sec)	9.20^{1}	6.67^{1}	2.07^{2}	4.41^{2}
Pauses/walk	0.47^{1}	0.22^{2}	0.21^{2}	0.16^{2}
Pecking bout (sec)	2.52^{1}	3.47^{1}	0.83^{2}	0.90^{2}
Pecks/pecking bout	1.25^{1}	1.04^{1}	1.61^{2}	1.92^{2}
Search bout (sec)	11.72^{1}	10.14^{1}	2.89^{2}	5.31^{2}
Pecks/search bout	0.188^{1}	0.20^{1}	0.459^{2}	0.320^{2}
Captures/peck	0.073u1	0.074^{1}	0.011^{2}	0.018^{2}
Captures/search bout	0.0092^{1}	0.0087^{1}	0.0028^{2}	0.0044^{2}
Handling time	2.30^{2}	4.46^{1}	1.32^{2}	2.30^{2}

* Like numerals indicate homogeneous groupings, as in Table 4.

However the mean daily intake of H. p. palliatus increases to 579 g/day during chick-rearing. This value is 98% of the male weight and 91% of the female weight. This substantial increase in the mean daily intake by H. p. palliatus in the chick-rearing period is again not possible for H. ater and H. p. durnfordi because the time available for feeding is restricted by the movements of the tide. These results support Lack's food limitation hypothesis interpreted as the amount of food available for the young.

3.3. Food limitation during pre-laying

Three variables that estimated the quality of the territory as a place to acquire food were matched with the reproductive performance parameters of the birds occupying those territories, to investigate whether local proximate factors affecting food availability during pre-laying could be related to reproductive performance. Data on territory quality and reproductive performance were obtained for 41 territories and a canonical correlation was computed between them. A high value for the first canonical variate measuring reproductive performance (REPRO1) indicated greater volume of clutches, more stable pair bonds, earlier clutch initiation dates, and shorter intervals between losing a clutch and beginning a replacement clutch (Table 6). Clutch initiation date had the highest linear correlation with the first canonical variate (REPRO1). High values of the first canonical variate measuring territory quality (TERR1) indicated large feeding areas on the territory, higher prey density on the territory, and closer distance to the feeding areas (Table 6). The latter variable correlated more strongly than other

TABLE 6. Summary of correlations between canonical variables for territory quality and reproductive performance, and raw variables for *H. p. palliatus*.

Variables	First Canonical variables for: Territory Quality[1] (TERR1)	Reproductive Performance[1] (REPRO1)
Size of feeding area on territory	0.63*	0.34
Distance from feeding area off territory	-0.82*	-0.45
Density of food on territory	0.35	0.19
Mean date of first clutch initiation	-0.35	-0.64*
Volume of replacement clutch	0.34	0.63*
Stability of pair bond	0.32	0.59*
Interval between loss of clutch and initiating replacement clutch	-0.30	-0.55*

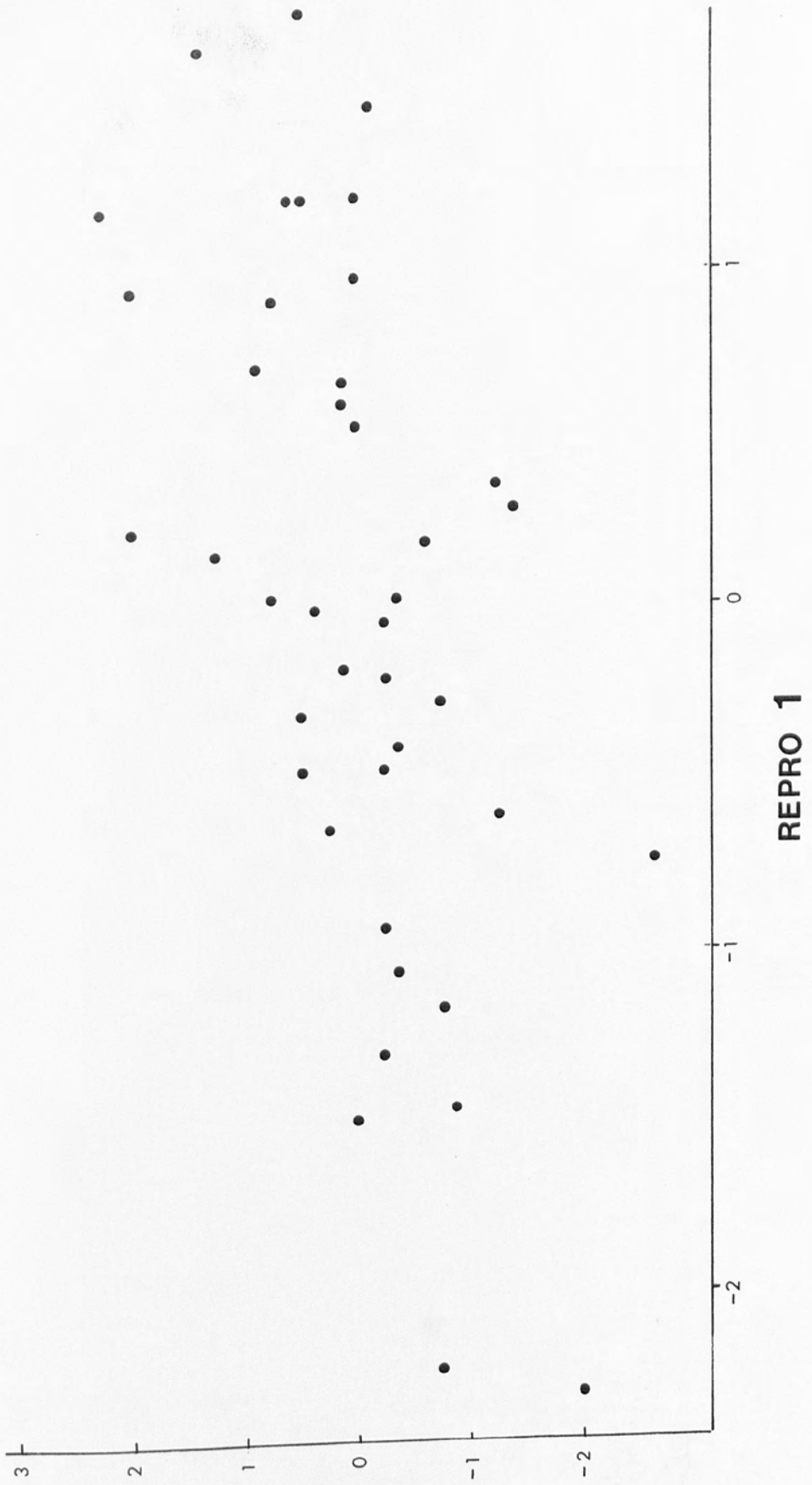
1 *- indicates $P < 0.01$.

territory quality measures with the first canonical variate. The correlation between the first canonical variates for reproductive performance values and territory quality values was positive, but only approached significance (canonical R^2=0.30, F=1.61, $P < 0.104$, Fig. 5). The food limitation hypothesis, interpreted as the amount of food available to the laying female, probably does not apply to oystercatchers. In the between species comparison the population with greater food intake during pre-laying had a smaller clutch size. Within H. p. palliatus territory quality, as it related to acquiring food during pre-laying did not appear to influence reproductive performance.

3.4. Environmental predictability hypothesis

Environmental predictability is examined using the following factors: predictability of feeding behaviour, variability in feeding behaviour, predictability in feeding paths, behavioural diversity, variability in egg parameters, and habitat and climatic stability. These are treated separately below.

Fig. 5. Plot of canonical correlation scores of territory holders for TERR1 against REPRO1 for H. p. palliatus.


TERR 1
3
2
1
0
-1
-2
-2
-1
0
1
REPRO 1

3.4.1. Feeding behaviour

If prey is distributed unpredictably in patches then the pattern of foraging should reflect that unpredictability (MacArthur and Pianka 1966). Eighty-six individuals (43 H. ater, 25 H. p. durnfordi, 18 H. p. palliatus) were observed feeding in over 7300 searching bouts. The prey varied in its distribution and I examined whether aspects of the feeding behaviour did reflect this variability and thus the predictability of the food supply.

Did walks or search bouts (Fig. 2) change over the course of time that I observed individual birds foraging? Serial autocorrelations (Box and Jenkins 1970) were run on the feeding variables for each individual with greater than 25 search bouts at lags of from 1 to 24. Less than 5% of the 448 correlograms examined contained significant autocorrelations, and these were usually only for the first few lags. Autocorrelations after five lags were in most cases insignificant. I interpret these results as indicating that variables remained unchanged over the foraging bout and that each search bout within a foraging bout could be treated independently. In all three subspecies future performance did not appear to depend on past performance in foraging, and as a corollary, future performance is as unpredictable as past performance.

I then tested whether successful pecking bouts (captures) influenced the length of successive walks, which might suggest area restricted search (Tinbergen et al. 1967), after a successful capture. Area restricted search indicates that the prey is distributed in patches and hence the environment may be less predictable if the locations of

the patches are unknown. I found a significant shortening of the length of the walk after a successful capture only in H. p. palliatus (Table 7). For controls I compared the length of previous walks and present walks when (1) the previous search resulted in no captures and the present search resulted in capture, (2) the previous search resulted in no captures and the present search resulted in no capture, (3) both searches resulted in captures. None of these three comparisons resulted in significant differences for any subspecies (Table 7).

I then examined the data for the presence of non-random successive long or short walks. Median walk lengths for individuals were used as the basis for categorizing walks as long (i.e., greater than the median), or short (i.e., less than the median, Zach 1977). A runs test (Sokal and Rohlf 1981) was applied to each individual and t-values of greater than 2.13 were taken as significant for all cases where the number of search bouts was greater than 15.

Twenty-three of 43 individuals of H. ater showed a non-random pattern in the foraging bout with runs of long, or short walks. In H. p. durnfordi, 10 of 25 birds had runs of long or short walks, and in H. p. palliatus 12 of 18 birds showed a non-random pattern of runs. These proportions did not differ significantly among the three subspecies (x^2 =3.05, P >0.05).

Did the relationships among the foraging variables change as a result of oystercatchers foraging on different prey items and do these relationships indicate anything about the way oystercatchers perceive their food supply? Correlation coefficients (r) were computed between all pairs of foraging variables for each feeding zone. In all zones, the

TABLE 7. Differences in length of walk under four possible combinations of successful and unsuccessful pecking bouts.

Success in: Last pecking bout	Present pecking bout	N	Species	Difference in length of walk between successive walks (sec)	t	P
No	No	1577	H. ater	-0.075	-0.44	n.s.
		800	H. p. durnfordi	-0.099	-0.25	n.s.
		1354	H. p. palliatus	-0.108	-0.61	n.s.
No	Yes	391	H. ater	0.109	0.25	n.s.
		256	H. p. durnfordi	0.068	0.12	n.s.
		50	H. p. palliatus	-1.17	-0.98	n.s.
Yes	Yes	420	H. ater	0.206	0.55	n.s.
		221	H. p. durnfordi	-0.423	-0.82	n.s.
		13	H. p. palliatus	-0.877	-0.28	n.s.
Yes	No	392	H. ater	-0.054	-0.12	n.s.
		256	H. p. durnfordi	0.586	1.06	n.s.
		50	H. p. palliatus	4.51	3.02	<0.004

number of pauses in the walk and the length of the walk were highly positively correlated (mean r=0.61) The length of the pecking bout and the walk were usually not correlated (mean r=0.13), but positively correlated in zone 4L for H. ater and zone 6M for H. ater and H. p. durnfordi. The length of the walk and the number of pecks in the subsequent pecking bout were not correlated in any zone (mean r=0.05), and the number of captures and the length of the walk were usually uncorrelated (mean r=0.12) but positively correlated in zone 6M for H. ater and in the Tagelus feeding areas of H. p. palliatus. The length of the pecking bout and the number of captures in that bout were positively correlated in all zones (mean r=0.43). The number of pecks in a pecking bout was positively correlated with the number of captures in zones 4L and 4M for H. ater and H. p. durnfordi; 5M for H. ater; zones 5L, 5M, and 6M for H. p. durnfordi; and in the Ensis and Crassostrea feeding areas of H. p. palliatus.

Positive correlations between the length of the walk and the length of the successive pecking bout in zones 4L and 6M may be a result of low densities of food occurring in patches. A bird may have more success if it moves farther from a previous site and searches there, particularly when the length of the pecking bout and the number of captures were positively correlated. It may pay, in the case of sparse food, for a bird to search actively longer after a long walk than after a short walk, because the short walk takes the bird less distance from an area already assessed, and presumably temporally depleted of prey. After a long walk into a new area it may pay to intensify the search by spending a longer period of time searching. In the case of homogeneous and abundant surface prey (e.g., Mytilus), or prey with an unknown distribution

(e.g., buried Ensis or Solen), this relationship need not hold because prey depletion is less likely to occur.

As a final test, using these data to determine whether past performance was related to future performance in feeding (and therefore predictability in feeding) in any of the zones defined here, I examined the pattern of captures within a pecking bout, and captures in the following pecking bout, in frequency tables. In a completely homogeneous environment the following should apply: the frequency of unsuccessful bouts following unsuccessful bouts (coded 0-0) as percentage of the total table should be inversely proportional to the density of food, the number of captures following (coded 0-1) or preceding (coded 1-0) unsuccessful bouts should be greater than the number of successive captures (coded 1-1). In a heterogeneous environment the frequency of (0-0) dyads should still be inversely proportional to the density of food, but the number of (0-1), and (1-0) dyads should be lower than the number of (1-1) dyads because two successive captures should be more frequent when an animal encounters a patch. These predictions are illustrated in Fig. 6.

According to this set of criteria, the birds are foraging in a way consistent with the classification presented in Table 8 for the 15 habitats. Because the two sympatric species may forage differently in the same habitats the results for each species are presented separately. The results for the sympatric H. ater and H. p. durnfordi agree only for zones 4M and 6M. In zone 5M the results agree for the measure of abundance of food, but not for the measure of distribution. This may be due to the birds actually using the habitats differently, or it may be due

Fig. 6. Predicted patterns of prey capture in oystercatchers for inferring patterns of distribution and abundance of prey, and thus the predictability of food resources. Zeros indicate unsuccessful search bouts, and ones indicate successful search bouts. The pattern represents a search bout in heterogeneous environments when prey is abundant (a), scarce (b), and moderate (c). The patterns represent search bouts in homogeneous environments when prey is scarce (a) and abundant (b).

Heterogeneous

a

1111101111011111111111

b

0001110000011100

c

0001111111100011111

Homogeneous

a

0000100001000000

b

0101010101010

TABLE 8. Classification of habitats by distribution and abundance of food, based on the pattern of successful and unsuccessful pecking bouts in *H. ater*, *H. p. durnfordi* and *H. p. palliatus*. N = total number of dyads.

Species	Zone	Classification: Distribution	Classification: Abundance	N	Percent of total dyads of form: 0-0	0-1	1-0	1-1
H. ater	4L	Homogeneous	Sparse	807	62.6	13.1	13.5	10.8
	4M	Heterogeneous	Mod.-Abund.	430	21.7	18.4	17.9	41.9
	5L	Heterogeneous	Sparse-Mod.	195	40.5	20.0	20.0	20.0
	5M	Homogeneous	Sparse-Mod.	403	58.1	15.1	14.1	12.7
	6M	Homogeneous	Sparse	791	74.6	10.4	9.6	5.4
H. p. durnfordi	4L	Heterogeneous	Moderate	133	22.6	25.6	24.8	27.1
	4M	Heterogeneous	Moderate	198	22.2	21.7	20.7	35.4
	5L	Homogeneous	Sparse	134	82.8	7.5	7.5	2.2
	5M	Heterogeneous	Moderate	157	43.3	14.0	14.6	28.0
	6L	Heterogeneous	Sparse	27	74.1	7.4	0	11.1
	6M	Homogeneous	Sparse-Mod.	884	59.4	16.6	16.4	7.6
H. p. palliatus	1M	Homogeneous	Sparse	169	78.7	9.5	9.5	2.4
	10	Homogeneous	Sparse	278	82.4	8.3	7.9	1.4
	1E	Homogeneous	Sparse	556	97.2	1.2	1.1	0.5
	1T	Homogeneous	Sparse	449	97.8	1.1	1.1	0

to the effects of sampling in slightly different habitats. There were some differences in the habitats in which I observed H. p. durnfordi and H. ater and although I attempted to observe H. ater feeding on H. p. durnfordi feeding areas and vice versa, both species were rarely observed feeding within the same zone. I suspect that differences in the habitats sampled, rather than in foraging behaviour account for differences in results for this zone, primarily because the results from the other mussel areas seem to concur for the two species.

By contrast, the behaviour of the two species while feeding on limpets did not agree in the classification of distribution or abundance of food. These results probably reflect differences in the facility with which the two species harvest limpets. H. ater appeared to harvest limpets in zone 5, where larger limpets were found, more efficiently than H. p. durnfordi. Conversely H. ater took limpets less efficiently than H. p. durnfordi in zone 4. H. ater appeared to move from rock to rock searching for limpets and consequently would be more likely to have two successive captures. As a result the habitat would appear heterogeneous. H. p. durnfordi was never observed specializing on limpets. These results agree with those of Baker (1974) who suggested that the shorter and stouter-billed oystercatchers in New Zealand were more efficient at harvesting limpets.

In all zones H. p. palliatus fed as if in a homogeneous environment, but the actual number of successful pecking bouts was low (Table 8). Food was classified as sparse in all habitats and part of this may be due to an actual low density of food. However, a sparse food classification could also result because the ratio of successful to unsuc-

cessful bouts was much greater in these habitats. For example, both Ensis and Tagelus recede into their tunnels out of reach, and are never clearly visible. H. p. palliatus must initiate many more pecks than H. p. durnfordi or H. ater for each successful capture. Mussels and oysters that are visible were captured in a higher proportion of pecking bouts (Table 8). Because Ensis and Tagelus are not visible H. p. palliatus cannot assess the abundance of the prey. The habitats containing these prey are therefore less assessable despite their apparent homogeneity than those containing mussels and oysters.

3.4.2. Variability in feeding behaviour

H. p. durnfordi and H. ater feed primarily on two prey species of different sizes whereas H. p. palliatus feeds predominantly on four prey species. The prey of H. p. durnfordi is visible and the abundance is probably visually assessed by the birds. If prey is clearly visible and limited in diversity this might affect life-history traits. Birds that can anticipate more accurately the amount of prey from year to year and season to season may apportion their resources to reproduction at a closer match to the resources available, than a bird that has a less assessable food supply. This generalization will be mediated by the abundance of prey. Presumably birds in unpredictable habitats with resources fluctuating to very low levels would not be able to produce a large number of eggs in anticipation of greater resources later.

The variability in the values obtained for the feeding variables might reflect the relative variabilities of the prey spectrums and the

degree to which the prey abundance can be assessed. In nearly every comparison of coefficients of variation of feeding variables of three taxa of oystercatchers (Table 9) even small differences were significant due to the very large sample sizes used. For all eight variables H. ater was more variable in feeding behaviour than H. p. durnfordi. For six of eight, H. p. palliatus was more variable than H. p. durnfordi, and for five of eight, H. p. palliatus was more variable than H. ater. In rate of capture, H. p. palliatus was the most variable and H. p. durnfordi the least. This result may be due to the broader spectrum of prey available to H. p. palliatus than either of the two other oystercatchers.

3.4.3. Analysis of feeding paths

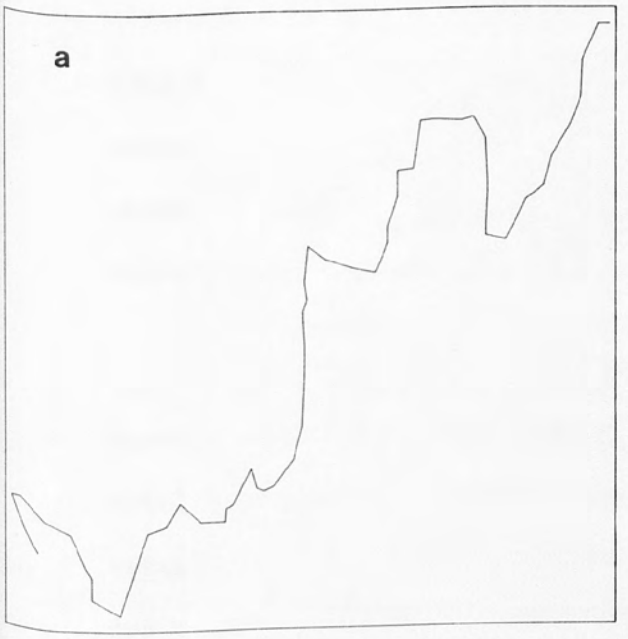
The shapes of feeding paths might reflect the birds' perception of the environment as predictable or unpredictable. If, as with the previous feeding variables, the paths indicate predictable prey distributions the birds might match their level of reproductive effort more closely to what is available. I mapped the feeding paths of 84 foraging individuals (52 H. ater and 32 H. p. palliatus). Examples of several paths from each of the two species are given in Fig. 7. Fig. 7a shows a typical path of a foraging H. ater moving through the mussel bed from the high to low water lines. The path is relatively directed. Most segments are quite short, and the locations of turns indicate where the bird has stopped to peck at mussels. Example 7b shows another H. ater feeding in zone 6. The path appears much more tortuous than example 7a, in part because the bird was forced back toward the high water mark whenever a

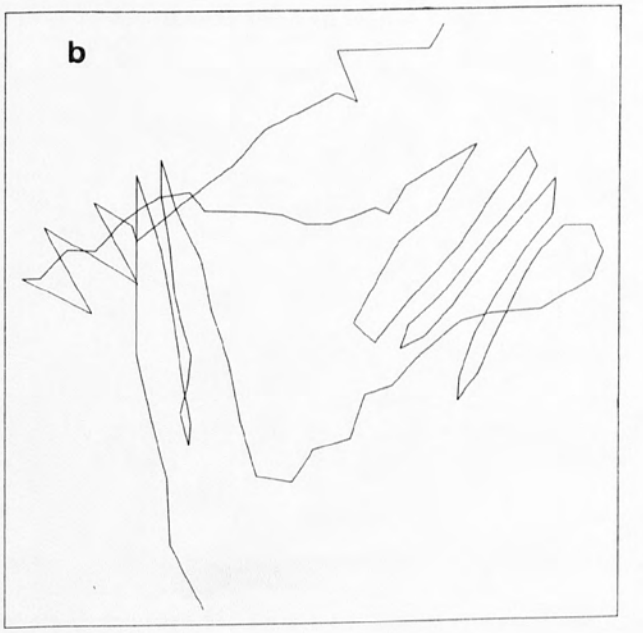
TABLE 9. Comparison of log-transformed coefficients of variation* (cv) in feeding variables between H. ater (n = 2923), H. p. durnfordi (n = 1563), and H. p. palliatus (n = 1962).

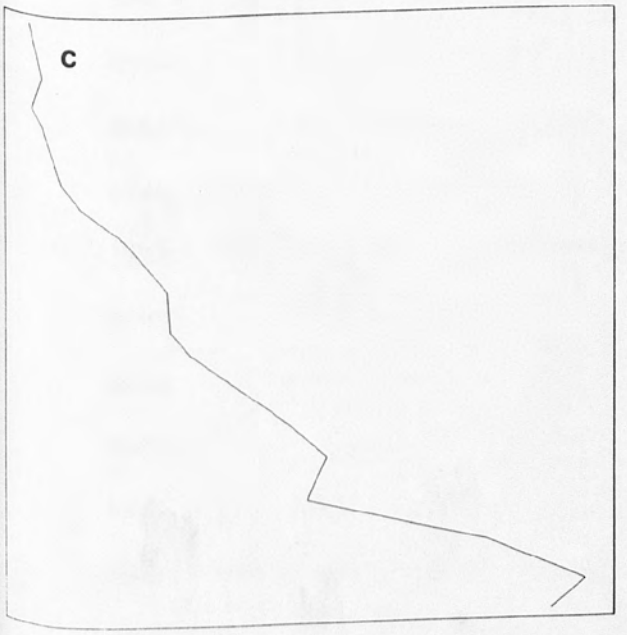
Variable	Comparison of: H. ater - H. p. durnfordi log-transformed cv	H. p. durnfordi - H. p. palliatus log-transformed cv	H. ater - H. p. palliatus log-transformed cv
Walk	1.908 > 1.872	1.872 < 1.877	1.908 > 1.877
Pauses/walk	1.790 > 1.654	1.654 < 2.019	1.790 < 2.019
Pecking bout	1.805 > 1.741	1.741 < 2.082	1.805 < 2.082
Pecks/pecking bout	1.821 > 1.742	1.742 > 1.595	1.821 > 1.595
Search bout	1.748 > 1.714	1.714 < 1.752	1.748 < 1.752
Pecks/search bout	1.833 > 1.646	1.646 > 1.613	1.833 > 1.613
Captures/peck	1.906 > 1.893	1.893 < 2.292	1.906 < 2.292
Captures/search bout	2.228 > 1.987	1.987 < 2.462	2.228 < 2.462

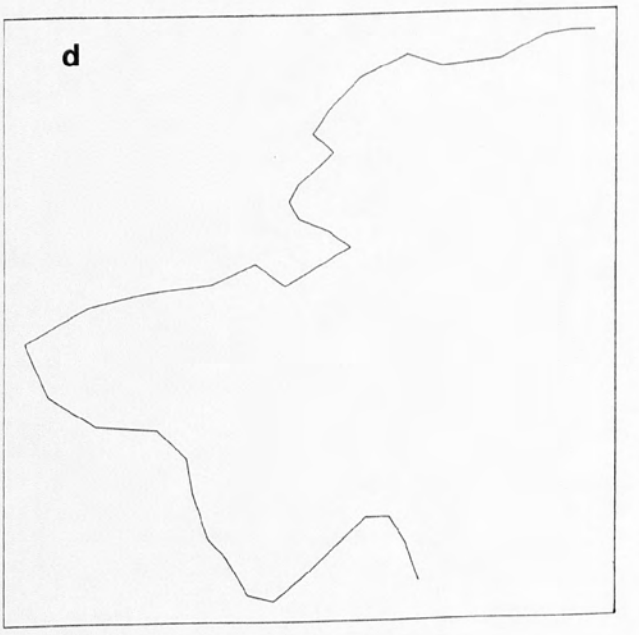
[1] Bader et al. 1966.

Fig. 7a-d. Four examples of paths of foraging individuals.


a


b


c


d

wave covered the previously exposed food items. Fig. 7c gives an example of H. p. palliatus feeding on a large mudflat containing Ensis clams. The birds' path is relatively straight. The bird cannot see the prey but walks and pecks nearly continuously on the mudflat. The final example (Fig. 7d) shows a H. p. palliatus feeding in a mussel area where the birds' search path follows the pattern of vegetation lining the clearing (see descriptions of feeding areas in Methods).

Differences in the lengths of segments of the paths between the two species were tested for. (Relative segment lengths as a proportion of total path length were compared because the scales of drawings varied between the two species and among individuals). These segment lengths are analogous to the search bouts in the previous analysis, and as with the search bouts, there was no significant difference in segment lengths between the two species (Table 10). Two measures of the tortuosity of search were then compared, because greater tortuosity might indicate area restricted search (Tinbergen et al. 1967, Croze 1970, Smith 1974a,b) and a more patchy environment. Tortuosity may be higher where prey is patchy, and lower where prey is distributed homogeneously. I used meander ratios which are calculated by dividing the beeline distance by the length of the total feeding path (lower values indicate higher tortuosity) and the fractal dimension (Table 10)(Mandelbrot 1983). Between the two species, these measures did not differ significantly. Neither of the two measures of tortuosity differed significantly among zones, and it appears that both species move through a habitat similarly regardless of the species of prey they are hunting. However, the speed at which H. p. palliatus moved through the habitats was about three times faster than the speed of H. ater (H. p. palliatus,

TABLE 10. Relative segment lengths, fractal dimensions,[1] and meander ratios,[2] for foraging paths of H. ater and H. p. palliatus. Mean ± S.E.

Variable	N	H. ater	N	H. p. palliatus	P
Relative segment[3] length	1599†	0.0478 ± 0.0025	977	0.0515 ± 0.0035	>0.05
Fractal dimension	52	0.4719 ± 0.0807	32	0.4669 ± 0.0682	>0.05
Meander ratio	52	0.471 ± 0.0394	32	0.541 ± 0.0556	>0.05

1 Fractal dimension = ln (total path length)/ln (beeline distance), Mandelbrot 1983;

2 Meander ratio = total path length/beeline distance; Zach 1977.

3 N = 1599 assumes independence of segment lengths within a path.

n = 5, x±S.D., 1.87±0.09; H. ater, n = 2, x±S.D., 0.46±0.10; t = 8.29, P < 0.001).

I then examined several aspects of successive turns (i.e., direction of turn (e.g., right or left), magnitude of angle of turn, and length of segment (e.g., short or long)) with three runs tests (Sokal and Rohlf 1981), as an additional means of assessing tortuosity. In none of these tests did the number of paths containing significant runs vary among the zones (Tables 11-13). To test for evidence of directedness in the paths I applied Rao's spacing test (Batschelet 1981). Directionality was found in all paths with over 15 segments and the occurrence of directional paths was not associated with any particular feeding zone. None of the components of the feeding paths varied among zones and indicated that the three taxa foraged consistently in habitats with apparently different prey distributions.

3.4.4. Behavioural diversity

If one species is better able to 'know' where and when it can feed than another, the former can be said to have a more predictable daily routine reflected in a more predictable daily allocation of time to different activities. Again, an ability to anticipate the daily activity budget and thus energy budget accurately might be reflected in a better fit between a birds' reproductive effort and the resources. The tide has a more pronounced influence on the behaviour of oystercatchers than does the daily cycle (see Chapter 3) because food is exposed by the tide. If the behaviour of all members of the population is affected

TABLE 11. Number of paths containing runs of right or left turns for each zone and species of oystercatchers.

Species	Zone	No. of paths in zone	No. of paths with sig. no of runs	Mean no of turns*	Mean 't' Value*	No. of - and + 't's -	+
H. p. palliatus	10	4	1	46	-3.39	1	0
H. p. palliatus	7	2	1	53	-2.20	1	0
H. p. palliatus	8	18	2	28	-2.83	2	0
H. ater	4	9	3	28	-2.617	3	0
H. ater	5	18	5	36.6	-2.714	5	0
H. ater	6	15	4	57.3	-2.275	4	0

* In paths with significant number of runs.

TABLE 12. Number of paths containing runs of wide or narrow angled turns for each zone and species of oystercatchers.

Species	Zone	No. of paths in zone	No. of paths with sig. no of runs	Mean no of turns*	Mean 't' Value*	No. of - and +
H. p. palliatus	10	4	2	20.5	-2.8	2
H. p. palliatus	7	2	1	53.0	-2.19	2
H. p. palliatus	8	18	12	33.4	-2.82	11
H. ater	4	9	6	25.7	-2.91	6
H. ater	5	18	12	33.0	-2.98	12
H. ater	6	15	6	55.8	-2.65	6

* In paths with significant number of runs.

TABLE 13. Number of paths containing runs of long or short segments for each zone and species of oystercatchers.

Species	Zone	No. of paths in zone	No. of paths with sig. no of runs	Mean no of turns*	Mean `t´ Value*	No. of - and + `t´s -	+
H. p. palliatus	10	4	2	3.15	-2.92	2	0
H. p. palliatus	7	2	2	38.0	-3.13	2	0
H. p. palliatus	8	18	8	36.0	-3.60	8	0
H. ater	4	9	4	26.5	-3.58	4	0
H. ater	5	18	14	41.7	-3.05	14	0
H. ater	6	15	10	55.9	-3.07	10	0

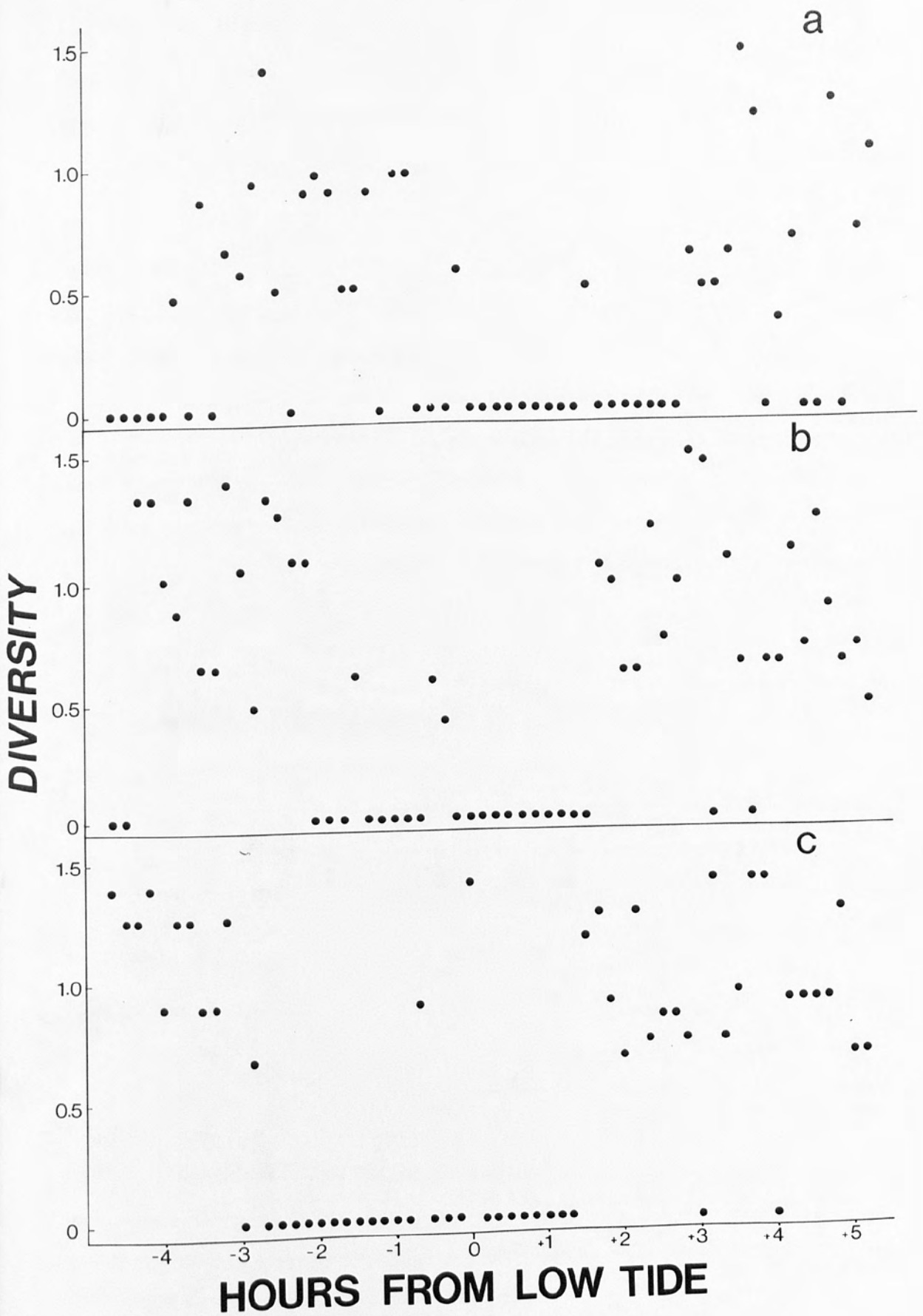
* In paths with significant number of runs.

equally and strongly by the tide, then diversity of behaviour patterns exhibited by the population at any time will be low because all birds will be engaged in the same activity. By contrast, if the tide has little or no effect on the activities of a group of birds, then the diversity of behaviour patterns should be high at any time. These trends should describe behavioural diversity when comparing two populations or species, if the underlying patterns of their synchrony (i.e., levels of social stimulation) are equal.

I measured the behavioural diversity in the populations by treating different behavioural acts as different 'species', in the classic use of diversity indices (Pielou 1975). I then calculated diversity indices every 10 min over the course of a tide cycle (12 h). I used the Shannon-Weaver diversity index because I was applying the method in much the same way it is applied in information theory; that is, to indicate roughly the behavioural options available to the birds at any point in time. In addition, the values for 'H' were highly correlated ($r2 > 0.94$) with other proposed measures of diversity (e.g., p_i^2, $1-p_i^2$, $1/p_i^2$, where p_i = the proportion of individuals in each category, i from the total number of individuals, May, 1976). Presumably all these measures represent the diversity in these data equally.

On all three days for which I observed H. ater or H. p. durnfordi over a complete tide cycle, the pattern of diversity indices was similar (Fig. 8). Relatively low diversity indices occurred around high water when most birds in the sample were on their nesting territories and were resting. The diversity in behaviour increased when the tide began to fall, when some birds were moving to the feeding areas. This transition

Fig. 8. Shannon-Weaver indices of behavioural diversity for two days of observations on H. ater (a and b) and one day of observation on H. p. durnfordi (c).

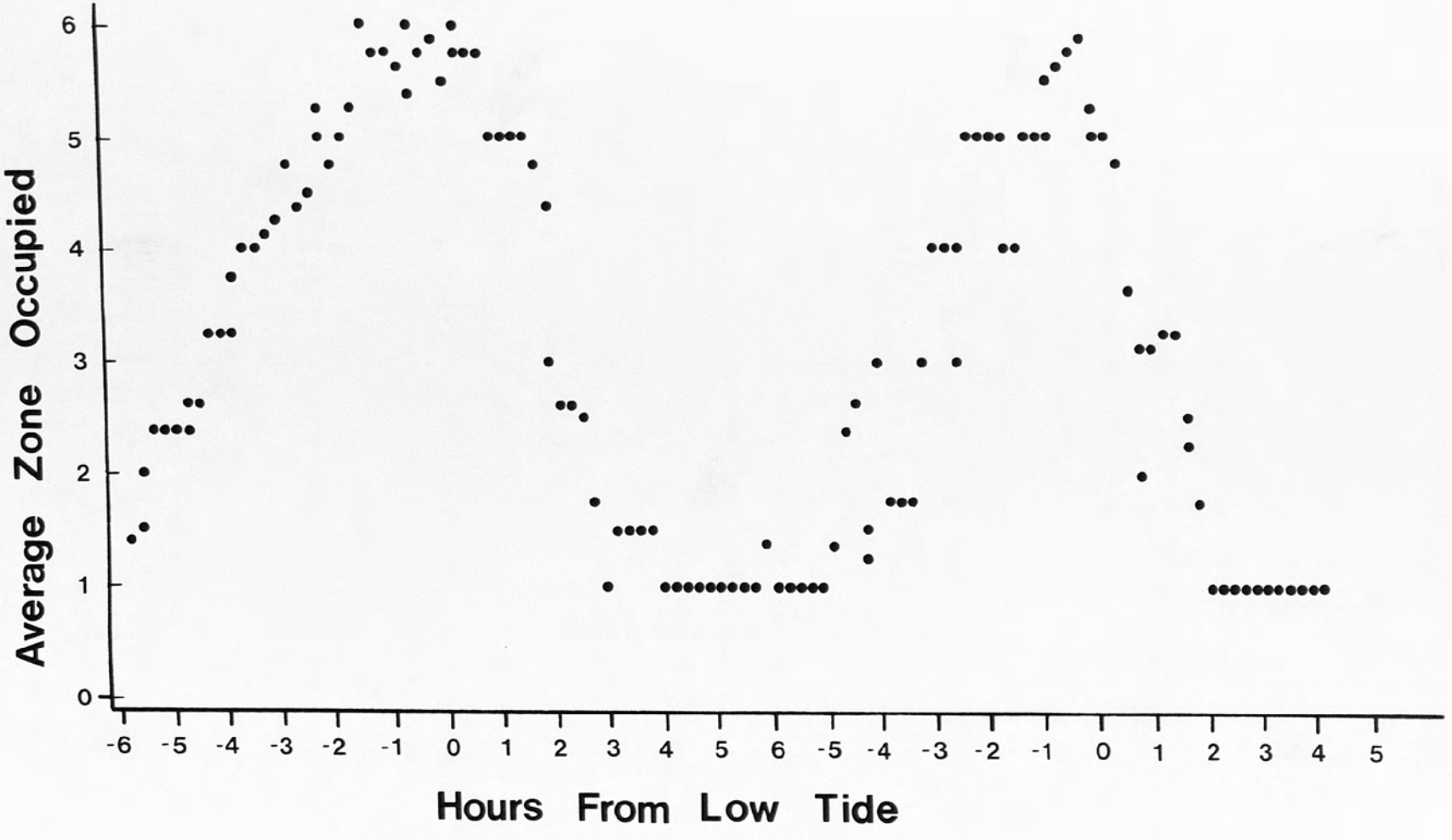

a
b
c
1.5
1.0
0.5
0
DIVERSITY
-4
-3
-2
-1
0
+1
+2
+3
+4
+5
HOURS FROM LOW TIDE

time is when most territorial disputes occurred in H. ater and H. p. durnfordi. Diversity in behaviour patterns declined to a minimum at low tide. When birds began to move back to their nesting territories there was an increase in the number of territorial disputes, other behavioural acts, and thus diversity. Near the time of high tide the diversity of behavioural acts once again declined as most birds again rested. The diversity patterns over the tidal cycle over several days approximates a sine curve, and hence shows regular oscillations in time.

H. ater moved from high on the nesting areas (at high tide) to the low water mark (at low tide), and the habitat zones that the birds occupied could usually be determined. The average zone occupied by all birds under observation was plotted against time (Fig. 9) and the two days of observation were joined. These data show sinusoidal cyclic oscillations with a period of about 12 hours, or the length of the full tidal cycle. A harmonic regression between time (converted to a cyclic variable, Legand 1958) and the percent of birds occupying each zone resulted in an R^2 of 0.57 ($n=132$, $F=173.1$, $P < 0.0001$), and indicated a high degree of predictability in which zone the bird occupied at any one time, given the time from low tide. Lack of clear zonation in the habitats of H. p. palliatus prevented me from doing similar analyses on the data from this species.

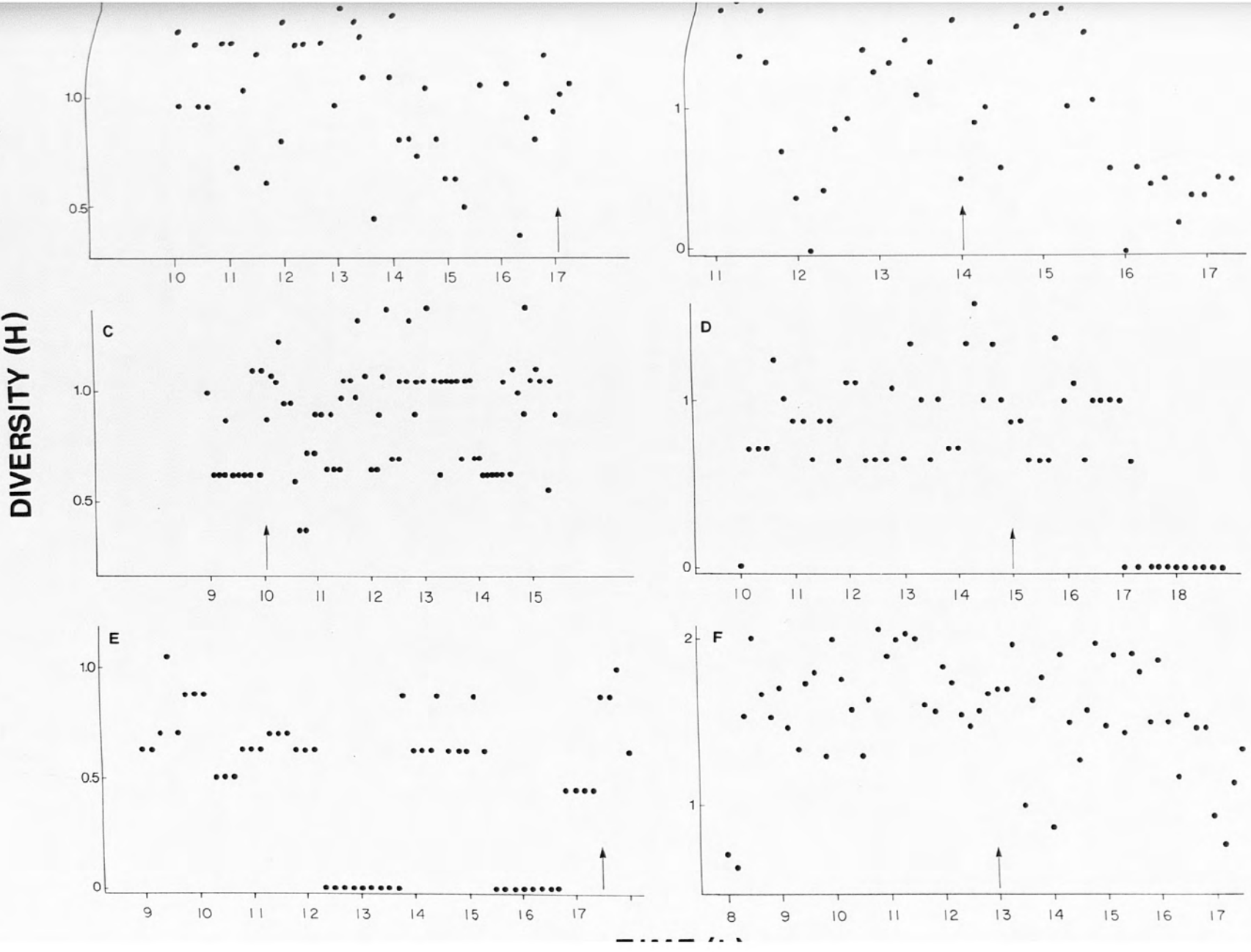
The interpretation of diversity indices over the tide cycle for H. p. palliatus in Virginia should be made with caution because when the birds were not on the territory, I assumed that they were feeding. Consequently when all birds were off the territory the diversity values given here probably underestimated the actual values. Scan sampling

Fig. 9. Average zone occupied by H. ater over two days of observation.


Average Zone Occupied
0
1
2
3
4
5
6
-6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 -5 -4 -3 -2 -1 0 1 2 3 4 5
Hours From Low Tide

sessions were conducted on 14 different days in the pre-laying period in Virginia, usually just for one half the tide cycle. I chose to plot only those six days for which I had the longest continuous periods of observation (Fig. 10). Only examples D and E show long periods when all birds under observation were engaged in the same act, (i.e., diversity of 0) but neither of these examples show a period of low diversity as long as that seen for H. p. durnfordi or H. ater, and neither patterns are clearly associated with the timing of the low tide. In example B there appears to be an underlying rhythmicity to the patterns of diversity, where a series of troughs occurs about every two hours. This apparent periodicity is not likely controlled by the tide. In examples A,C,D and F, there appears to be no relationship between diversity of behaviour patterns and the pattern of the tide. H. p. palliatus forages in the inter-tidal zones but the zones in Virginia are more diffuse and availability of the inter-tidal prey is not clearly restricted in time, as it is in Argentina.

Fig. 10. Shannon-Weaver indices of behavioural diversity for six partial days of observation of H. p. palliatus.


DIVERSITY (H)
C
D
E
F

3.4.5. Variability in egg parameters

One of the basic assumptions in the literature on brood reduction in birds is that its occurrence is strongly associated with habitats where the food is unpredictable in time and space (Ricklefs 1965, Howe 1976). The assumption may not be true and the regular loss of one or more chicks from differential allocation of parental resources may, for example, be only a form of insurance in the event of infertility of one of the other eggs, regardless of the predictability of the resource (e.g., Warham 1974, Graves et al. 1984). The presence of consistent egg-size ordering or large egg-size variability within a clutch is usually associated with brood-reduction (Howe 1976), but may simply result in a more efficient way of provisioning food to chicks (Hahn 1981). However, variability in egg parameters within a clutch might indicate less certainty by the parents of matching resources to the requirements of the brood (Crump 1981), at least relative to a species with similar forms of parental care but less variability in egg size. Variability in clutch initiation dates might reflect the time available to breed and this should correlate with the length of the breeding season.

Variability in egg parameters among the three subspecies were compared using pairwise F-tests on coefficients of variation transformed with log transformations (Bader and Lehmann 1965). Within-clutch variability for egg length, egg breadth, shape and volume were estimated with the value of the mean square from replications (i.e., eggs within a clutch) rather than the mean square error. There was no clear trend in the comparison between H. ater and H. p. durnfordi, with the latter having greater intra-clutch variability in egg breadth ($P < 0.001$) and H.

ater having greater variability in egg length (Table 14). The eggs of H. p. palliatus were more variable ($P < 0.05$, Table 14) in every parameter than those of H. p. durnfordi or H. ater.

I then checked for egg-size ordering in 20 clutches of H. ater and four clutches of H. p. durnfordi, and found no evidence for any systematic pattern in size between first and second (and third) eggs in either species, although the sample for H. p. durnfordi was really too small for this result to be conclusive. Egg-size ordering does occur in the clutches of H. p. palliatus. First and third eggs are about equal in size and second eggs are larger (Chapter 2).

There is some yearly variation in clutch initiation dates (Chapter 2) so I compared the mean coefficients of variations from three years with the coefficients from the one year study on H. ater and H. p. durnfordi. In all three species clutch initiation dates were equally variable (Table 14).

TABLE 14. Comparison of within-clutch coefficients of variation (cv; log-transformed) in egg parameters of *H. ater* (n = 73), *H. p. durnfordi* (n = 56), *H. p. palliatus* (n = 298)[1].

Parameter	Comparison of: *H. ater* - *H. p. durnfordi* log-transformed cv	F[1]	*H. p. durnfordi* - *H. p. palliatus* log-transformed cv	F	*H. ater* - *H. p. palliatus* log-transformed cv	F
Egg length	0.7353 > 0.1383	5.32**	0.1383 < 0.9225	6.67**	0.7353 < 0.9225	1.25
Egg breadth	0.1237 < 0.4158	3.36**	0.4158 < 0.5738	1.38	0.1237 < 0.5738	4.64**
Egg shape	0.6902 > 0.3186	2.17*	0.3186 < 0.8939	2.82**	0.6902 < 0.8938	1.29
Egg volume	0.8187 > 0.7017	1.17	0.7017 < 1.0600	1.51	0.8187 < 1.0600	1.29
Egg weight	0.5686 < 0.5823	1.02	0.5823 < 1.1003	1.89*	0.5686 < 1.1003	1.94*
Clutch initiation date	1.2450 < 1.4415	1.16	1.4415 > 1.3549	1.06	1.2450 < 1.3549	1.09

[1] ** $P < 0.005$, * - $P < 0.05$

3.4.6. Reproductive success

1984: 11 nests monitored
0 hatched

Reproductive success was low for all three taxa. In Virginia, the eggs in 32 of 229 nests hatched (13.9%). At least one chick fledged in 22 of these 32 nests (68.7%). In five broods all three chicks fledged, in nine broods two chicks fledged and in eight broods one chick fledged. In Argentina eggs in one of the twenty nests of H. ater hatched (5%) and one chick fledged. Eggs in three of 12 nests of H. p. durnfordi hatched (25%). Whether these chicks fledged is unknown. Flooding by periodic spring tides and predation were the main causes of nest loss in Virginia. Predation by Southern Polar Skuas (Catharacta skua) and Dominican Gulls (Larus dominicanus) was the major cause of nest loss for both species in Argentina.

3.4.7. Habitat variability

Several habitat sampling techniques were used to estimate variability in the habitats of the three taxa and to measure the degree of predictability in finding prey by oystercatchers. In all five transects from high to low water marks in Argentina the total number of mussels tended to increase with distance from the high water mark, but declined suddenly at a distance of 10 to 30 m from the low water mark (Fig. 11). The size of the mussels also increased with distance from the high water mark (Fig. 12). The same trend was found in comparing the transects from H. p. durnfordi and H. ater territories separately. Mussels increased in size with distance from the high water mark (mussel sizes

Fig. 11. Mean number of mussels from five transects plotted against the distance from the high water mark on Punta Tombo, Argentina.

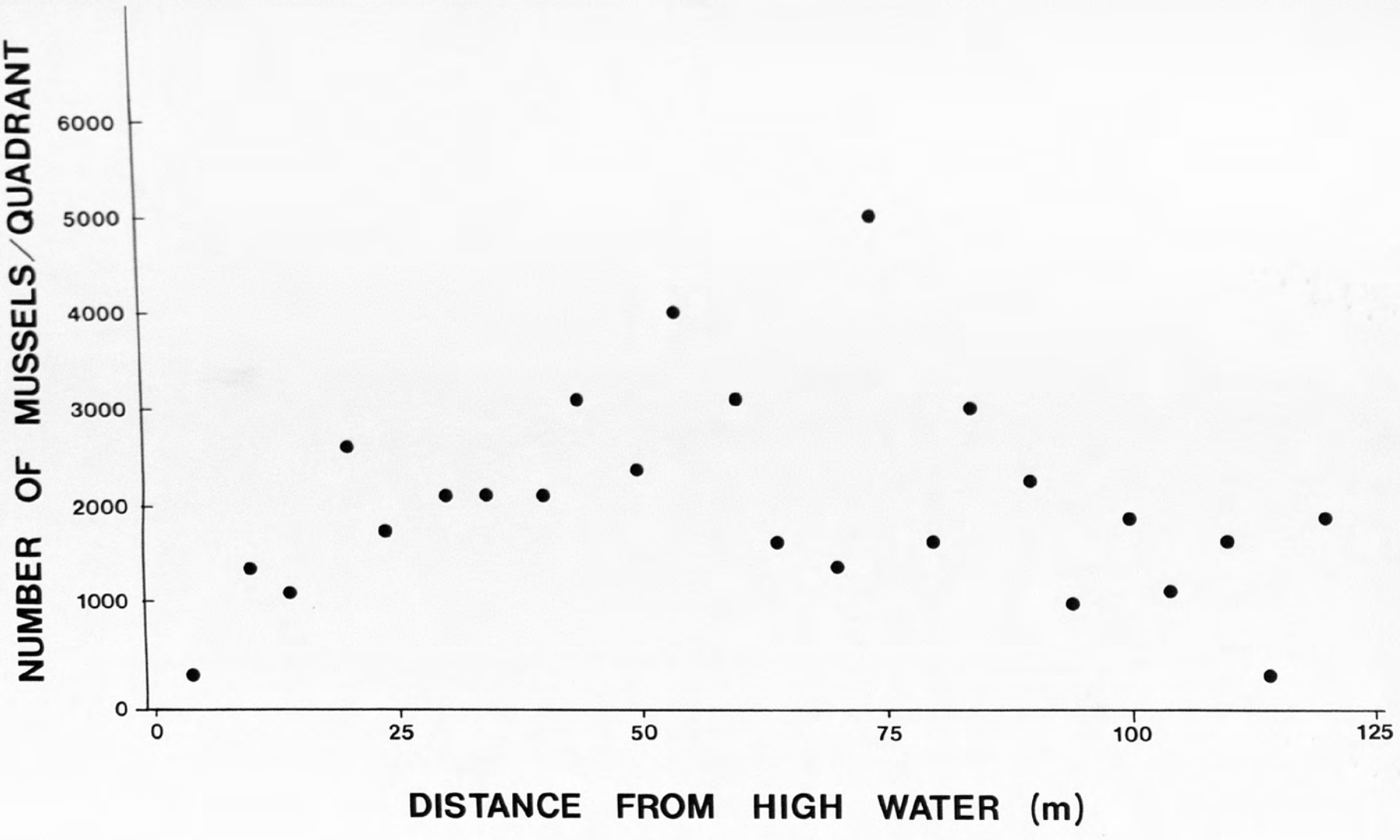
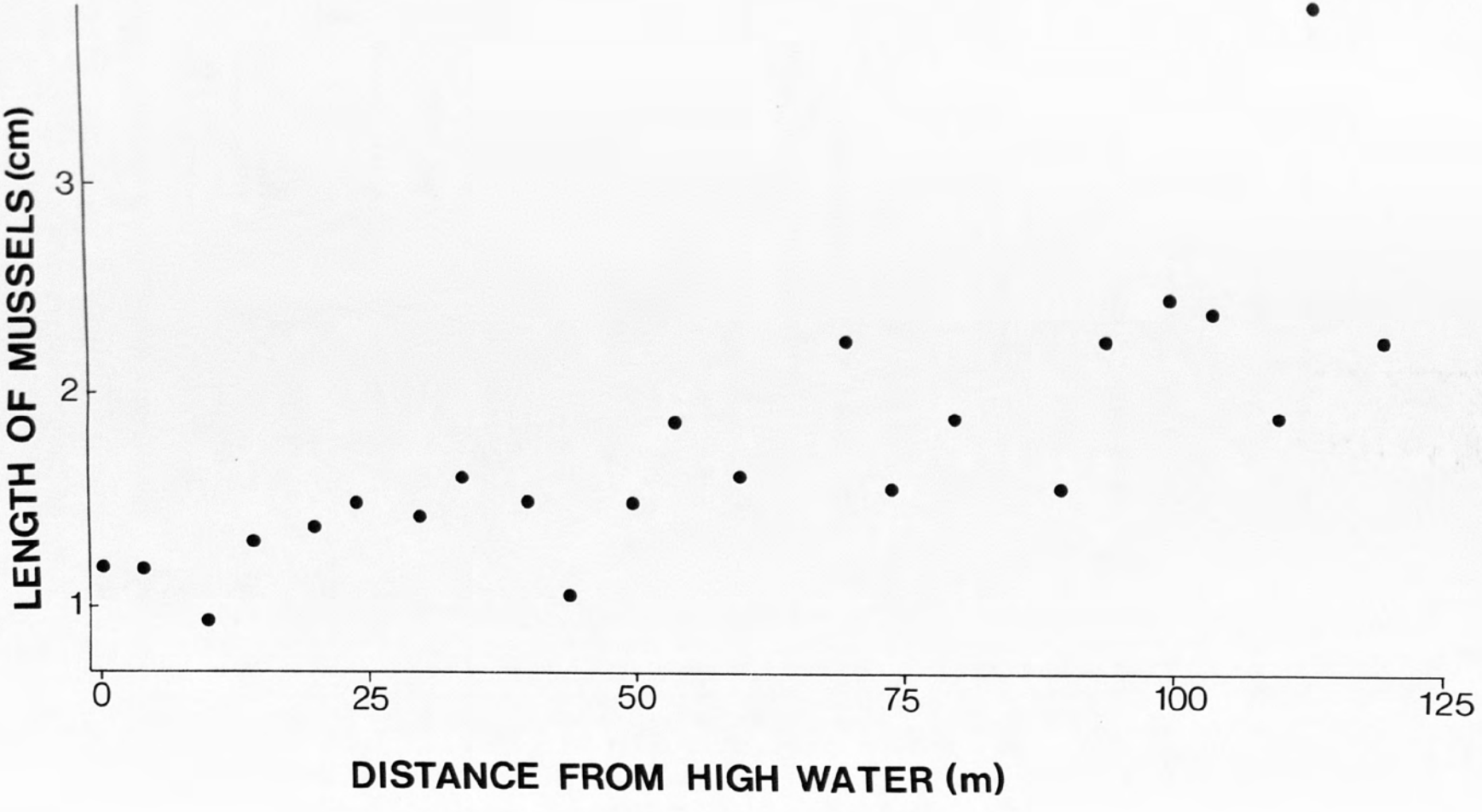

NUMBER OF MUSSELS/QUADRANT
6000
5000
4000
3000
2000
1000
0
0
25
50
75
100
125
DISTANCE FROM HIGH WATER (m)

Fig. 12. Mean size of mussels from five transects plotted against the distance from the high water mark in Punta Tombo, Argentina.


LENGTH OF MUSSELS (cm)
3
2
1
0
25
50
75
100
125
DISTANCE FROM HIGH WATER (m)

from three transects on H. ater territories plotted against distance from high water mark, F= 24.83, R^2=0.43, P < 0.0001, n=33 quadrats; mussel sizes from two transects of H. p. durnfordi territories, F=13.17, R^2=0.43, P < 0.0025, n=17 quadrats). The transects for H. ater and H. p. durnfordi did not differ significantly in numbers of small Modiolis, large Mytilus or size of these mussels (ANOVA, P > 0.05).

The number of limpets present along the transect lines also increased with the distance from the high water mark, but declined suddenly at varying points depending on the transect line. The mean number of limpets along five transects is plotted in Fig. 13 and indicates low predictability in finding a given density of limpets at any one distance from the high water mark (R^2=0.02). No limpets greater than 1 cm in diameter occurred until a distance of 55 m from the high water mark. Of 216 limpets occurring in five transects at distances 55 m or greater from the high water mark only 9 were greater than 2 cm. Most limpets here were about 1 cm in diameter.

Rectangular plots of prey densities were used to measure spatial heterogeneity within territories, and to measure the 'match' between habitat structure and prey density. Rectangular plots consisted of four parallel transects, extending from the high to low water marks, each at a distance of 10 m apart. I tested for correlation in the number of limpets and mussels, percent rock, water, and lichen across transects within plots, and across transects between plots.

In general, correlations among prey densities within plots were higher than correlations among plots (Table 15). A Kruskal-Wallis test with plot as the class variable reaffirmed the results of the

Fig. 13. Mean number of limpets from five transects plotted against the distance from the high water mark in Punta Tombo, Argentina.

NUMBER OF LIMPETS
10
5
0
0
25
50
75
DISTANCE FROM HIGH WATER (m)

TABLE 15. Spearman rank correlations between prey and habitat variables within transects and between habitat plots for *H. ater* and *H. p. durnfordi*.

Variables	Plot #1		Plot #2		Plot #1-Plot #2	All data
	Mean r[1]	r	Mean r	r	Mean r[2]	
No. of limpets - % mussels	0.357	0.447[3]	0.286	0.116	0.229	0.412[3]
No. of limpets - % rocks	0.204	0.226	0.244	0.221	-0.115	0.112
No. of limpets - % water	-0.034	-0.050	0.137	-0.014	0.102	0.114
% mussels - % rocks	-0.250	-0.214	-0.352	-0.543[3]	0.044	-0.370[3]
% mussels - % water	-0.017	-0.084	-0.056	-0.219	-0.009	0.029
% rocks - % water	0.017	0.051	-0.205	-0.261	0.114	-0.175

1 Mean of correlations from 4 transects.

2 Mean of values from 2 correlations, e.g., mean of r for limpets plot 1 - mussels plot 2 and limpets plot 2 - mussels plot 1.

3 $P < 0.001$

correlations, with significant differences between the two plots (using the quadrats on the four transects as replicates) ($F=3.65$, $P < 0.05$).

In Virginia, the habitats in the salt marsh were of relatively even elevation and with the falling and rising of the tide, the feeding areas were evenly and quickly exposed or covered by water. Mussels (Modiolis) lived in areas that were often not covered by the tide during the course of a day, but would usually be inundated during the monthly spring tides. As a result mussels were often available throughout the day.

The distribution of mussels did not appear to be related to the distribution of grasses. In four rectangular plots of salt marsh the correlation between the amount of grass (mostly Spartina alternifolia) (scored from 1-no grass to 4-dense grass) was low: plot 1, $r=0.59$, $P < 0.01$; plot 2, $r=0.13$, n.s.; plot 3, $r=0.02$, n.s.; plot 4, $r=0.35$, $p < 0.04$. In two of four plots there were weak correlations between the amount of grass and the prey density, with higher numbers of mussels being associated with dense grass. Overall, for the four grass classes there were no significant differences in the number of mussels (ANOVA, $F= 0.83_{3,116}$, $r=0.02$, $P > 0.05$).

For each plot I then computed serial autocorrelations to examine overall heterogeneity of the plots (Table 16). Autocorrelations among grass quadrats were consistently higher than autocorrelations among prey quadrats, and often significant. Autocorrelations among prey quadrats were higher for adjacent rows and columns than for other rows, but only once were the prey densities in two rows significantly correlated. This result suggests that the habitat was more homogeneous than the prey. However, this result occurs, in part, because of the lower variability

TABLE 16. Significance of serial autocorrelations among quadrats in plots measuring densities of *Modiolis* and *Spartina* (plots 1-3) and *Ensis* (plot 4).

Plot no.	N	To Lag	Prey density Chi-square	P	*Spartina* density Chi-square	P
1	28	6	9.32	0.156	18.90	0.004
		12	12.32	0.421	22.71	0.030
		18	21.65	0.248	41.47	0.001
		24	24.62	0.426	66.88	0.000
2	65	6	16.47	0.011	58.11	0.000
		12	20.50	0.058	111.82	0.000
		18	23.54	0.171	149.47	0.000
		24	24.60	0.428	182.84	0.000
3	27	6	2.15	0.905	25.57	0.000
		12	4.55	0.971	46.06	0.000
		18	9.26	0.953	57.14	0.000
		24	25.86	0.360	61.68	0.000
4	32	6	1.04	0.984	-	-
		12	3.42	0.992	-	-
		18	5.60	0.998	-	-
		24	14.30	0.939	-	-

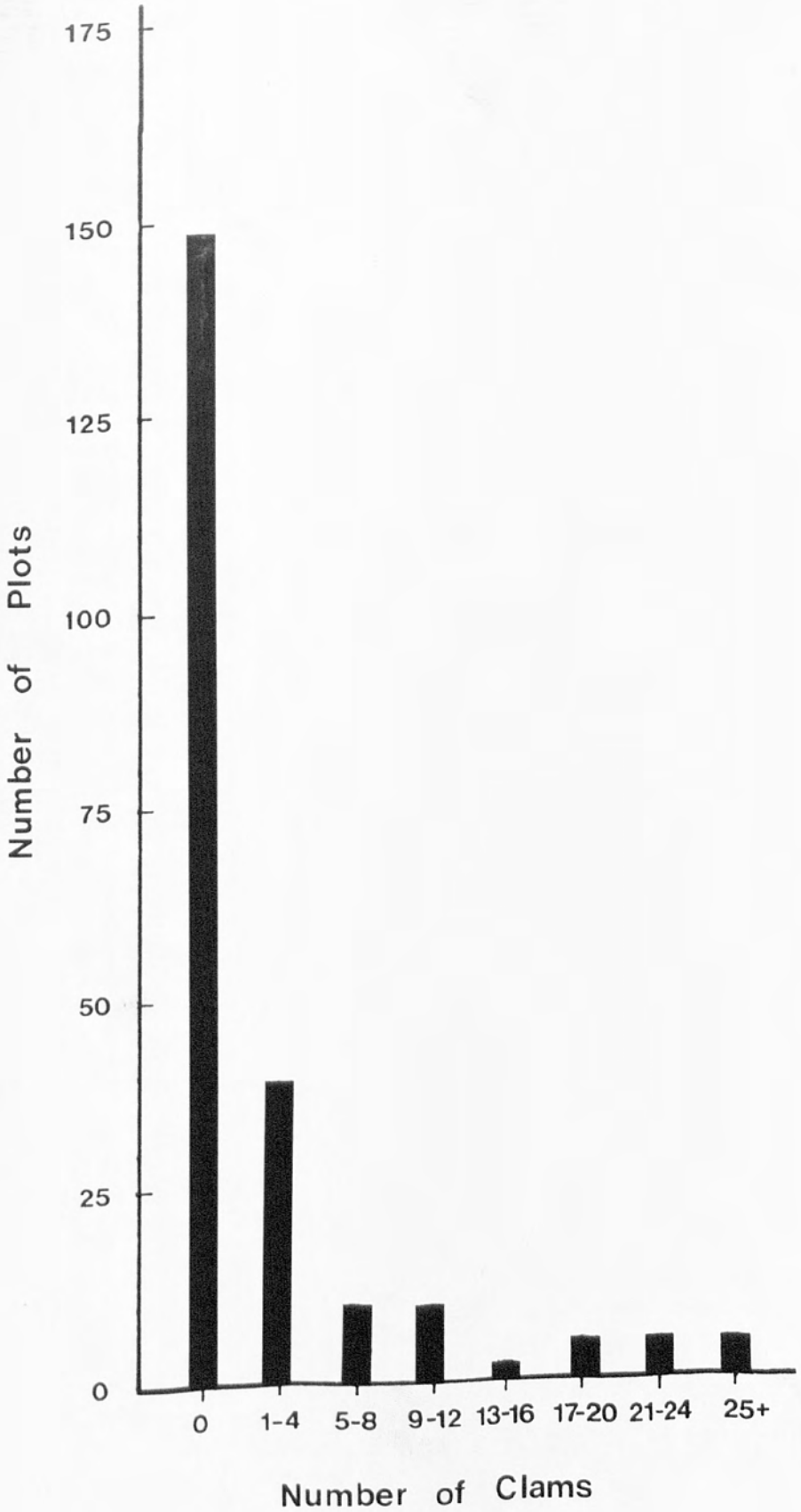
in the values of grass classes then in mussel numbers. The plots containing Ensis clams were more heterogeneous than the plots containing mussels. These clams appeared to occur randomly throughout the plots.

I sampled in areas containing Tagelus sp. razor clams (i.e., mudflats free of vegetation) with randomly placed quadrats. The frequency distribution of the number of Tagelus sp. in 208 randomly placed quadrats is given in Fig. 14, and shows that most quadrats are empty and only a very few contain large numbers of Tagelus.

3.4.8. Comparison of predictability across habitats in space and time

Comparison of predictability among six rectangular plots on H. p. palliatus territories and two plots on H. ater/H. p. durnfordi territories was made using the value $P = t_{ij}/n - p_{ij}/n$ where t_{ij} is the number of quadrats in the plot that contain prey, n is the number of quadrats in the plot, and p_{ij} is the probability of encountering a prey item from any point within a rectangular plot if the searcher makes one move to any other quadrat point within the plot. The searcher can move any of eight possible directions if moving from the centre of the plot, five directions from the boundaries, and three possible directions from the corners. The value p_{ij}/n approaches the value of t_{ij}/n when the probability of encountering prey is high in a plot. High values of P occur when the probability of encountering prey within a plot is low. I treated the distribution of limpets separately from the distribution of mussels. In four prey sampling plots on Punta Tombo $P=0.01 \pm 0.001$, and was significantly lower than in six plots in Virginia ($P=0.043 \pm 0.001$,

Fig. 14. Frequency distribution of the number of Tagelus plebeius in 208 randomly placed quadrats in coastal Virginia.


175
150
125
100
75
50
25
0
Number of Plots
0
1-4
5-8
9-12
13-16
17-20
21-24
25+
Number of Clams

t=4.38, d.f.=8, $P < 0.001$), indicating that prey is generally more predictable in space in Argentina than in Virginia.

In Virginia the location of sand bars (Maurmeyer 1981), and hence prey, changed measurably from year to year. The distribution of mussels was more constant from year to year but was still affected by the changing currents and winter storms. In contrast the distribution of mussels and limpets on the rocky intertidal areas of Punta Tombo appeared to be very similar in 1982 to what they were in 1981; they occurred densely and covered most rock surfaces. The relative stability of these two habitats relates to the stability of the substrates (e.g., sand in Virginia, basaltic rock in Argentina).

3.4.9. Climatic stability

Predictability has two components, constancy and contingency (Colwell 1974). The best measure of constancy of a climate appears to be the measure of the difference between mean July and mean January temperatures (MacArthur 1975). This value averaged over 20 years of data (1963-1982) from Trelew, Chubut, Argentina ($43^{o}14'S$, $65^{o}19'W$) is 15.5^{o}. The corresponding value from Snow Hill, Maryland is 21.8^{o} C. The climate in Maryland and Virginia fluctuates more widely, and hence is less constant than the climate of central coastal Patagonia. Contingency can be assessed using the mean monthly and yearly standard deviations of temperatures. These standard deviations are significantly higher in Virginia than in central Patagonia (monthly comparison: Va,. S.D. = 1.65, Arg., S.D. = 1.27, t= 2.49, $P < 0.02$, d.f. = 22; yearly

comparison, Va., S.D. = 8.06, Arg., S.D. = 5.51, t= 15.16, $P < 0.0001$, d.f. = 38). This result indicates that there is less certainty in predicting the temperature for any given month or year in Virginia than in central Patagonia.

4. Discussion

4.1. Food limitation hypotheses

The results from this study demonstrated only a weak relationship between territory quality and reproductive performance. Therefore, little support was found for the food limitation hypothesis as expressed as the amount of food available for the female during pre-laying. The comparison among the three taxa also failed to provide support for this hypothesis. Both species in Argentina fed more during pre-laying but laid smaller clutches than H. p. palliatus in Virginia. However, the availability of food for the laying female is probably not the most important determinant of modal clutch size in oystercatchers, because they feed their young (despite having relatively large eggs). Therefore the more appropriate test should be a comparison of food available to the adults for chick-rearing. In this comparison my data supported Lack's hypothesis because H. p. palliatus (with a larger mean clutch size) fed at a slightly higher daily rate than the two species (with smaller mean clutch sizes) in Argentina. However, the second prediction of equal availability of food for the chicks and thus equal clutch sizes

was refuted because the two species in Argentina had approximately equal access to food for the chicks. Lack's hypothesis may only be adequate to explain within-species variability in clutch size.

The results from several studies of H. ostralegus concur with those found here. Food limitation does appear to influence brood size and therefore may influence minor clutch size variation. Safriel (1967) found that birds feeding young on a limpet diet reared significantly fewer chicks (0.16/pair) than birds feeding young on a terrestrial diet (0.95/pair). Heppleston (1972) compared inland and coastal populations of H. ostralegus with accessible and inaccessible food respectively. Heppleston found a higher proportion of first clutches with 3 or 4 eggs at the inland site, higher mean clutch sizes at two inland locations than at one coastal location in one year, and that inland replacement clutches were smaller than first clutches, corresponding to a decline in food availability at the inland site later in the season (food at the coastal location remained high). He also found earlier laying at inland sites than at coastal locations, and a higher number of chicks fledged per pair at inland sites than at one coastal location. The latter difference was attributed to differences in the efficiencies with which the adults were able to care for the chicks (Heppleston 1972) and not to differences in the amount of food available to the parents. Recently Briggs (1984) reported the same trends between coastal and inland breeding birds in Lancashire, England. In the Black Oystercatcher (H. bachmani) Groves (1982) also found that birds feeding young from food available on rocky inter-tidal areas could not easily support three young. Young from one chick broods grow faster than young from two chick broods (Groves 1982, 1984).

If Lack's hypothesis is sufficient to explain the reduced modal clutch size of oystercatchers breeding in Argentina then selection must act against those females laying first clutches of three eggs. About 30% of the H. p. durnfordi in Argentina still lay first clutches containing three eggs. These birds are not selected against either because the cost of laying the extra eggs is too small, or they are exceptionally good parents and do occasionally raise three young. The latter possibility seems unlikely since the evidence from other studies (Groves 1982,1984) indicates that three young are almost never raised on rocky substrates. As well all three broods of H. p. durnfordi which I observed contained only one chick, although each clutch they hatched from contained three eggs. The energetic cost of egg-laying is probably so low (about 500 kj / egg spread over 10 days) that selection acts not on those individuals which lay three eggs but only on those which rear three young. Since raising three young is a relatively rare event selection against those individuals that lay three eggs is probably also rare.

4.2. Environmental predictability hypothesis

The results of this study indicated that there were measurable differences in the predictability of habitat and behaviour between the two subspecies of H. palliatus and these differences were consistent with the predictions of the environmental predictability hypothesis. The breeding population of H. p. palliatus in Virginia can be characterized by irregular feeding schedules and few time restrictions as to when individuals can forage, resources distributed unpredictably in space and time, widely fluctuating spring tides that can result in no reproductive success in any one year, relatively low climatic stability, short migration, variable egg dimensions, egg-size ordering within clutches, and large variance in the number of offspring raised in any one year. By contrast, H. p. durnfordi has a rigorous daily feeding pattern related to the movements of the tide, birds are restricted to feeding when all other conspecifics at the locality feed, and resources are distributed predictably along a gradient from low to high tide, and predictably in space from year to year. The birds experience high climatic stability throughout the year, do not migrate (Jehl et al. 1973), there is no evidence of egg-size ordering within clutches, they have low mean clutch size, and probably a low number and variance in number of young. The environmental predictability hypothesis differs from Lack's hypothesis because it implies feedback on individual survivorship from reproduction. Individuals which lay small clutches when adult survivorship is unpredictable, and those which lay large clutches when adult survivorship is stable should be selected against. In this study the environment for the adults was certainly more stable in Argentina than in Vir-

ginia and one can then surmise that adult mortality is greater in Virginia than Argentina because of greater environmental perturbations in the former. However, I have no evidence that this is so. Adult mortality figures for H. p. palliatus and H. ostralegus are basically inconsistent with the hypothesis of environmental predictability acting on adult survivorship and consequently acting on clutch size. H. ostralegus has higher survivorship than H. palliatus (90% per annum, Safriel et al. 1984 vs. 85% per annum, see Chapter 3) but also lays the same size clutch (Table 17). The evidence for a relationship between fecundity and adult survivorship within a species is weak (De Steven 1980, Hogstedt 1981, Smith 1981) and survivorship may play a less significant role in the evolution of clutch size (Tuomi et al. 1983) than always assumed (Cody 1966). Environmental predictability acting on adult survivorship between two populations of oystercatchers is probably too complex an explanation to invoke here. Environmental predictability probably has a greater effect on resources (stable in time and space at a relatively low level in Argentina and unpredictable in time and space but at a higher level, in Virginia), than on adult mortality patterns. Variability in resources is probably the simplest explanation for clutch size variation within the species H. palliatus.

TABLE 17. Clutch size, growth parameters, and egg volume/body weight ratios in 4 species of oystercatchers.

	Mean size of first clutch	Mean no. of chicks[6]	Max. daily mass increment (g)	Mean adult weight (g)	Clutch volume/ adult weight
H. p. palliatus[1]	2.78	1.32	15	602	0.19
H. bachmani[2]	2.04	0.54	7.5	640[7]	0.14
H. ostralegus[3]	2.71	1.58	17.0	531[8]	0.20
H. ostralegus[4]	-	-	11.1	-	-
H. moquini[5]	1.81	0.42	15.6g	694g	0.14

1 - This study.

2 - Groves (1982), ROM collection.

3 - Heppleston (1972)

4 - Webster (1942)

5 - Hockey (1983b)

6 - Mean number of chicks fledged per pair with hatched eggs.

7 - ROM skin collection.

8 - Mean adult weight, March (Dare 1977).

4.3. Life history comparisons of *H. ater* and *H. p. durnfordi*

H. ater and *H. p. durnfordi* have similar reproductive attributes in that the modal clutch size of each species is two eggs, with each egg constituting about 6.5% of female body weight. As well, both birds share the same feeding habitats, although the variability of all feeding parameters was greater in *H. ater* than in *H. p. durnfordi*, and the behaviour in most feeding zones was distinguishable between the two species. The behavioural response to the tide in both species was similar, with a distinct daily pattern of feeding directly related to the movements of the tide.

Within-clutch coefficients of variation in egg parameters were comparable in both species, with neither being consistently more variable than the other, and in neither species was there any evidence for egg-size ordering. However, clutch size in *H. p. durnfordi* was more variable as this subspecies laid three eggs in 32% of the nests.

Differences in mean clutch size and clutch size variability probably can not be attributed to differences in food uptake, since I found that the uptake of food expressed as a percentage of body weight was very similar in the two species. There are several other possible explanations for this difference in mean clutch size and range of clutch sizes. First, clutch size appears to be related to brood size (Table 17), and *H. p. durnfordi* may be better able to rear more young than *H. ater*. Second, density-dependent feedback on clutch size may be operating to suppress clutch size in *H. ater*. Thirdly, clutch size may be inversely related to body size and thus *H. ater* lays fewer eggs because

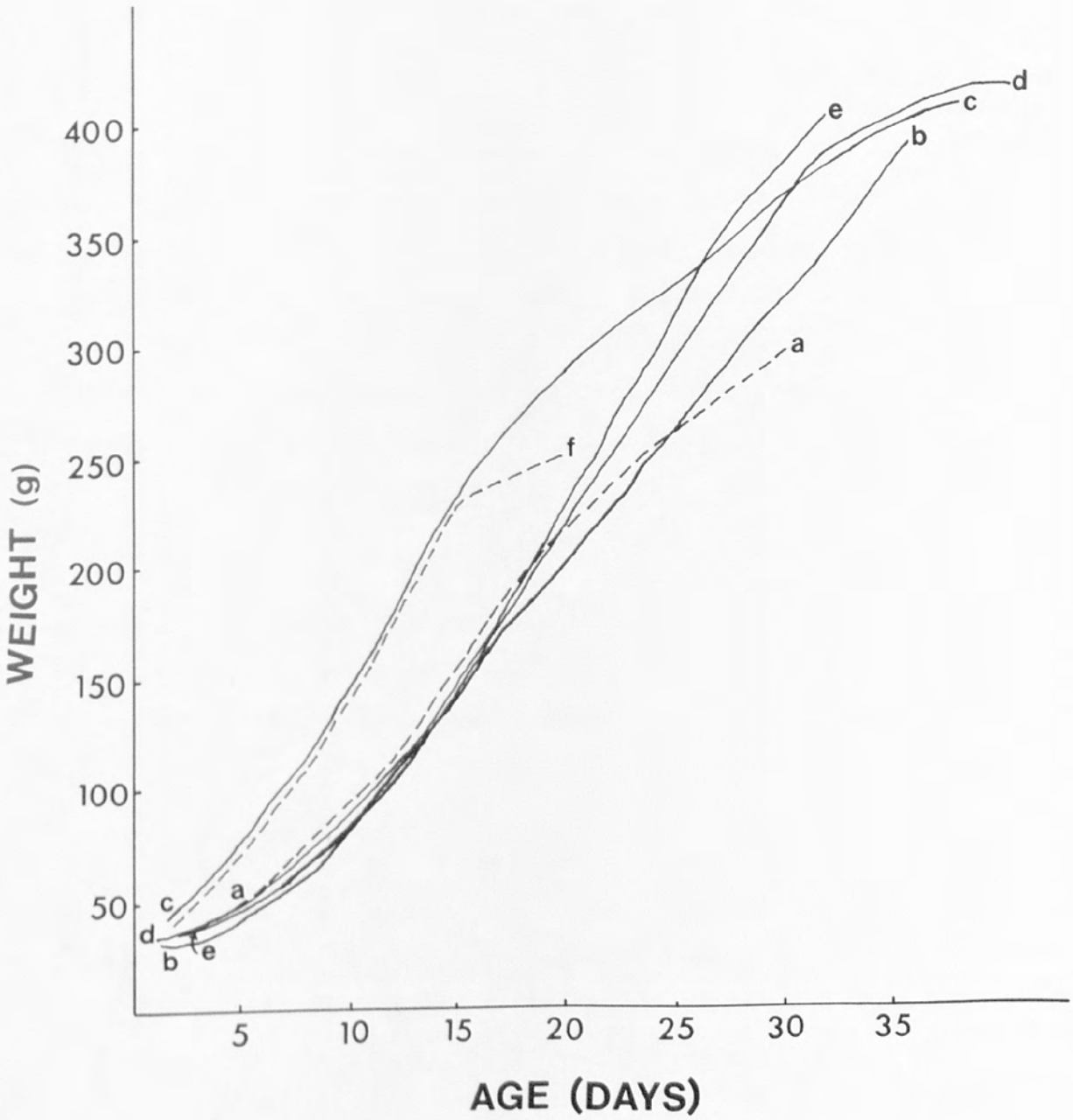
it is larger. Fourthly, the two patterns of clutch size are related to environmental predictability outside the breeding season.

Finally, phylogenetic constraints could explain the differences in maximum clutch size (vis a vis Stearns 1983a, 1984). This means that within a clade (e.g., H. palliatus) it is reasonable to look for differences in clutch size in terms of limiting factors like food. However, in a different clade that has evolved at a different time and place, clutch size differences may be correlates of the morphological differences that define the two species.

The first explanation seems unlikely, in that the parental behaviour of both species appeared to be very similar. Parents of both species led their young to the high tide line shortly after hatching, and brought food to them there. After several days, the young follow the foraging adults around in the inter-tidal zone. Anti-predator behaviour of the two species is similar (Miller and Baker 1980) and growth rates, if they follow the trends in all other widely divergent oystercatchers (excepting H. ostralegus, Fig. 15), are probably also similar.

The second explanation suggests that the H. ater population is closer to its carrying capacity (K) than H. p. durnfordi, and hence is producing less. This explanation is an extension of the explanations for differences in life-history traits across all taxa: the classic r- and K-dichotomy (MacArthur and Wilson 1967), with H. ater experiencing more density-dependent mortality than H. p. durnfordi. How do the data for other species of oystercatchers fit with this explanation? The prediction is that those species that nest in high densities will have

Fig. 15. Growth rates of four species of oystercatchers: H. bachmani (a) (Groves 1982), H. bachmani (b) (Webster 1942), H. ostralegus (c) (Heppleston 1972), H. p. palliatus (d) (this study), H. moquini (e), (Hockey 1984), H. ostralegus (f) (est. from Safriel 1981).


WEIGHT (g)
400
350
300
250
200
150
100
50
5
10
15
20
25
30
35
AGE (DAYS)
a
b
c
d
e
f

lower average and maximum clutch sizes. The data for ten populations are summarized in Table 18 and indicate that there is a relationship among species between the density of the breeding population and clutch size. All taxa with low average clutch sizes (< 2.1 eggs), nest in densities of over 0.5 pairs/ha. In the intra-specific comparison the relationship breaks down. Inland breeding H. ostralegus in North Lancashire lay a modal clutch of three eggs and also nests in high densities. H. p. palliatus in Virginia had a modal clutch of three eggs and nested at higher densities than H. p. durnfordi.

Nest-site availability may be the simple explanation for differences in nesting densities of the various species. H. moquini appears to be restricted to offshore islands due to human disturbance elsewhere (Hockey 1983a) and hence the high densities may be an artifact of this restriction. There is some evidence that H. unicolor in New Zealand nests in low densities outside areas of human disturbance, and high densities when humans occur on their preferred habitat (Baker pers. comm.). When forced to nest in dense situations, oystercatchers may appear to be more tolerant of conspecifics. Behavioural tolerance is probably a fairly plastic trait in oystercatchers. Variability in density within a single species suggests that density-dependent mortality is not a major influence on clutch size in this group.

For there to be a cause and effect relationship between high density and low clutch size it has to be shown that birds that have more than one or two young are selected against as a consequence of a large number of conspecifics. In practical terms this translates into territories having too few resources to support, for example, three young, or

TABLE 18. Relationship between density of breeding populations in ten populations of oystercatchers.

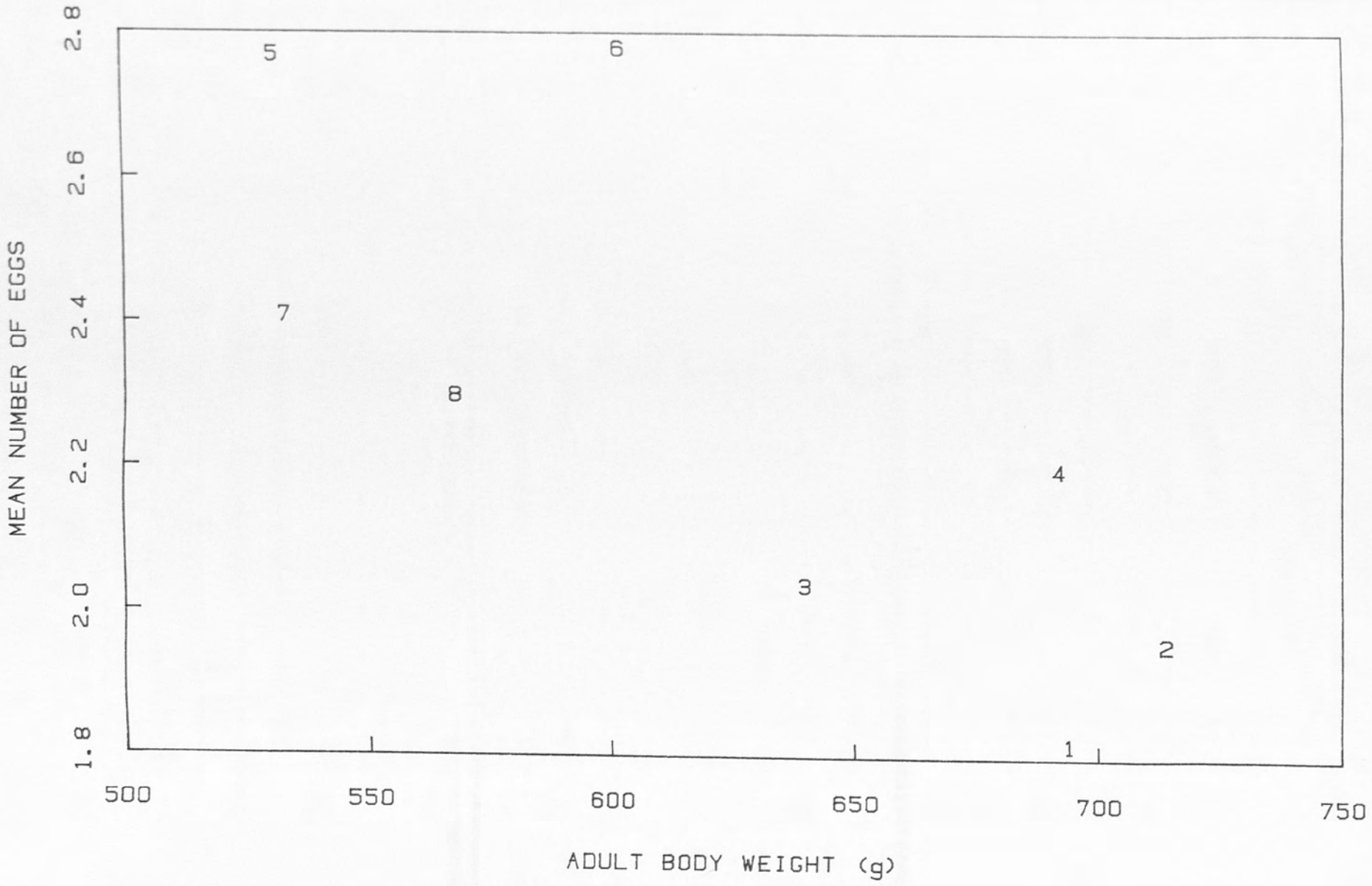
Species	Number of pairs/ha	Location	Mean clutch size	N
H. p. palliatus	0.27	Chincoteague, Virginia	2.78	129
H. p. durnfordi	0.16	Punta Tombo, Argentina	2.31	22
H. ater	0.50	Punta Tombo, Argentina	1.96	41
H. bachmani	2.12	Cleland Island, British Columbia	2.04	310
H. moquini	0.68	Marcus Island, South Africa	1.82	84
H. ostralegus	0.14	Forvie Reserve, Scotland	2.56	52
H. ostralegus	0.05	River Ythan, Scotland	2.77	143
H. ostralegus	1.47	Riperian, North Lancashire, Eng.	2.70	142
H. ostralegus	0.02	Agrarian, North Lancashire, Eng.	2.80	29
H. ostralegus	0.11	Coastal, North Lancashire, Eng.	2.60	89

the effects of a larger number of young increasing territorial aggression, which in turn increases predation on the young. There is some evidence that those territories occurring adjacent to rocky inter-tidal areas cannot support three young (Groves 1982), but the number of young appears to be limited by the maximum feeding rates of the adults and no the availability of the prey on the territory. For the second factor t be important a positive relationship between territorial aggression and brood size needs to be demonstrated. This relationship appears to be negative in H. p. palliatus (pers. obs.).

The number of young may also be limited on rocky territories with few hiding places by the ability of the parents to care for more young (e.g., Safriel 1975, Lenington 1980, Walters 1982), or by increased pre dation on these territories. These factors may be influenced by an increase in conspecifics by reducing the number of available hiding places for the young. However, lower densities of the black forms H. unicolor and H. moquini in some locations again suggest that increased nesting densities are not the sole cause of lower maximum and average clutch sizes in oystercatchers.

Can the larger size of H. ater and the other species laying a maximum of two eggs (Fig. 16), account for the smaller clutch size? With the available information this possibility can not be discounted. Stearns (1983b, 1984) found that size accounted for much of the variation in life-history traits in lizards and mammals. However, this did not negate the possibility that the primary force of selection as a result of local conditions, was on body size, followed by coadaptive adjustments in other life-history traits (Stearns 1983b). Large body

Fig. 16. Bivariate plot of mean adult weight and clutch size for seven populations of oystercatchers: H. moquini (1), H. ater (2), H. bachmani (3), H. unicolor (4), H. ostralegus (5), H. p. palliatus (6), H. p. durnfordi (7), H. o. finschii (8).


MEAN NUMBER OF EGGS
2.8
2.6
2.4
2.2
2.0
1.8
5
6
7
8
4
3
2
1
500
550
600
650
700
750
ADULT BODY WEIGHT (g)

size may be associated with other life-history traits, but can also be considered another trait influenced by a given environment. The questions 'Why are the species that lay only two eggs, larger?' and 'Why do some species only lay two eggs?' then become equivalent.

The literature on Haematopus taxonomy is quite confused. Larson (1957) proposed that oystercatchers originated as dark-plumaged birds in Eurasia, and emigrants from this stock moved south during the Pleiocene and established themselves as new (isolated) species. Subsequently, most of the original stock mutated to pied forms and a second southerly migration of pied birds occurred during the Pleistocene. These birds settled, sometimes in areas where black forms had already been established but were (are) able to coexist due to the evolution of the older black forms. Baker (1977) found no evidence for the above scenario, and on analyzing the morphometrics of the genus, concluded that two sister groups of Haematopus exist. These are distinguishable on the basis of eye-ring and back coloration (i.e., yellow-eyed, brown-backed form, and red-eyed, black-backed form). The melanism has probably arisen independently in several geographically widespread taxa (Baker 1977). Jehl (1968) concluded that the melanistic forms are adapted to the nest substrate. Dark young are less conspicuous on rocks, and become black adults. Support for this view comes from the fact the predation during the chick stage accounts for most of the variability in reproductive success among pairs, in at least some species (Heppleston 1972, Groves, 1982, pers. obs.). Black adults on dark substrates may also be less prone to discovery by egg predators during incubation.

There does not seem to be a clear phylogenetic difference l black and pied forms. However, there are ecological correlates t black or pied which can have acted on the life-history traits bc and clutch size, presently, in the past, or at both times. Thus genetic constraints as a result of previous selection may have s the respective life-histories of black and pied forms.

The dichotomy of rocky substrates vs. sandy substrates appe be the only consistent correlate in oystercatchers for those spe which are melanistic, large and usually lay only two eggs, and t tercatchers that are pied, small and can lay three-egg clutches. ater is like H. bachmani, H. moquini, H. unicolor and H. fuligir inhabiting rocky coasts, in living at high densities, in having clutch of only two eggs, and in not migrating and having limited in colonizing new areas (Table 19). These characters are in con those possessed by H. palliatus (five subspecies), and H. ostral (seven subspecies)(Baker 1973), both species which have invaded habitats worldwide. These species lay three eggs and rarely fou migrate, and they live in ephemeral habitats. Under nearly iden feeding conditions, H. p. durnfordi did not nest in large number Punta Tombo, but nests on beaches up and down the southern Atlan coast whereas H. ater requires rocky outcrops and its distributi restricted to areas physically similar to Punta Tombo (Blake 197 range of H. p. durnfordi is more restricted than that of H. ater palliatus inhabits a much larger range than H. ater (Heppleston Wide ranging organisms usually have greater genetic variability hence greater adaptability than species with restricted ranges (

TABLE 19. Known maximum clutch size, nest site preferences, migration patterns and ranges of ten species of oystercatchers.

Subspecies	Maximum clutch-size	Nest-site preferences	Migration pattern	Range
H. p. palliatus[1]	4	Sandy or pebbled beaches	Migratory	North and Central America
H. p. durnfordi[2]	3	Sandy or pebbled beaches	Resident	Coast of southern South America
H. ater[3]	2	Rocky beaches	Resident	Coasts of southern and cent. S. A.
H. bachmani[1]	3	Rocky beaches	Resident	West coast of North America
H. moquini[4]	2	Rocky beaches	Resident	Coasts of South Africa
H. ostralegus[5]	4	Sandy or pebbled beaches	Migratory	Iceland, Scand., to Spain
H. unicolor[6]	3	Sandy beaches, rocky platforms	Resident	South Island, New Zealand
H. o. finchii[6]	4	Sandy or pebbled beaches	Migratory	New Zealand
H. chathamensis[6]	3	Rocky beaches	Resident	Chatham Islands
H. fuluginosis[7]	3	Rocky beaches	Resident	Australia
H. longirostris[7]	3	Sandy or pebbled beaches	Resident	Australia
H. leucopodus[3]	2	Meadows, sandy beaches	Resident	Southern South America

1 AOU checklist 1983, 2 This study, Baker 1973, Jehl et al. 1973; 3 Wood 1975; 4 Hockey 1983; 5 Cramp 1983; 6 Oliver 1955; 7 Slater 1971

and Cooper 1984). The ranges of the larger, usually black, rock-inhabiting forms are generally restricted (Hockey 1983b).

Stearns (1980) and others have found the clearest examples of co-varying life history traits at higher taxonomic levels, and this has led Stearns to suggest that life-history 'tactics' per se are correlated with patterns of covariation in morphological traits, and hence, not, as originally perceived, responses of selection on a suite of characters in a certain ecological context. However, in a recent review of data on mammal life-history traits, Stearns found that although much of the variation in life-history traits explained by the first principal component disappeared when the effects of phylogenetic constraints (e.g., family and order) and body size were removed, the relative loadings of each trait on the first principal component did not change. The first principal component described the classic 'r' and 'K' continuum of Pianka (1970), Tinkle et al. (1970) and Cody (1971), with early maturing, small short-lived animals with short gestation periods, and many small altricial young at one end, and large mammals with the opposite set of characters at the other end. He concluded, therefore, that as one progressed through genera and into species, the loadings of the traits would probably still hold on this first principal component, but would hold for fewer and fewer traits. He concluded that this finding indicated an adaptive basis to the dichotomy.

In oystercatchers I have examined a few life-history traits, and it would be ideal to know about differences in longevity, age at maturity, and mortality rates of chicks, juveniles and adults, to test for covariance among the traits and to test for their characteristics in the

predictable-unpredictable habitat spectrum. The underlying assumption in all explanations of the differences in clutch size between the groups is that these above life-history traits also differ, providing there is a large enough cost associated with laying more eggs. Size appears to be one life-history trait that covaries inversely with clutch size. Longevity in birds is a function of body size (Calder 1974) and possibly the black forms do live longer. However, survival costs of laying an extra egg in H. p. durnfordi may be negligible and hence not subject to intense selection.

Brown (1983) found that intra-specific differences in the life-history traits of fresh-water snails in different environments were smaller than the differences among species. However, this may be because, as Brown (1983) suggested, when more unlike organisms are compared, there should be more differences in life histories. Brown did find slight differences in the life-history traits of snails which were correlated with different ecological conditions (i.e., temporary vs. permanent ponds).

In two species of Daphnia, Schwartz (1984) found that one species living in predictable environments produced more and smaller young earlier than a second congener living in measurably less predictable conditions. These latter individuals matured later and had smaller brood sizes. This trend is predicted by life-history theory only if predictability is lower for the juveniles than for the adults. An unpredictable environment for the adults should correspond to early maturation and large numbers of offspring. In this study the effects of predictability were mediated by the specific effects of predation and temperature on

mortality.

In an experiment manipulating densities of Drosophila pseudoobscura, the predictions of life-history theory were only weakly met (Taylor and Condra 1980). In another study on Tisbe fuscata, Bergmann (1984) showed that density-limitation favoured increased fecundity, a prediction opposite to that of the classic r- and K-selected association of traits, but consistent with a theory based on selection in age-structured populations (Charlesworth 1980). A similar finding resulted from manipulating cultures of Escherichia coli in different densities (Luckinbill 1984). Adaptation for rapid growth occurred in groups with low and high densities and Luckinbill (1984) concluded that the same adaptations would be selected for regardless of the classic association of life-history traits.

Is there evidence from the vertebrates for evolution of life-history traits at lower taxonomic levels than family or order? Proximate factors, rather than selection, were cited as responsible for deferring reproduction, slow growth and greater competitive ability of Gila topminnows (Poecilipsis occidentalis) in a more predictable environment (Constantz 1979). Some inconsistencies in the association of life-history traits were found with some fish in the more constant environment maturing faster than fish in a widely fluctuating environment. Stearns (1983b,c) examined life-history traits of mosquitofish (Gambusia affinis) in fluctuating and stable environments. Many of the differences were attributed by Stearns to plastic responses of the organisms that shared similar genetic potential. However, the life-history characteristics he found to have a genetic basis were the opposite set of

those predicted by life-history theory. Female mosquitofish from stable reservoirs were larger and younger at maturity and had smaller offspring than females from fluctuating reservoirs. In a more detailed analysis of specific characteristics of the reservoirs (e.g., size, volume of water, average percent full), Stearns concluded that rapid fluctuations selected against large fish, while fewer fluctuations selected for more, larger offspring. In both studies of fish the traits of early maturation, and high fecundity did not necessarily go with short lives and small young, or vice-versa. In both studies the predictable/ fluctuating environment dichotomy may have been too broad and may have masked other more specific factors in the environment that influenced life-histories in one or several directions.

The establishment of the relative survival costs of particular life-history strategies is the crucial link for progress to occur in the study of life history evolution, and this component has barely been touched. The lack of solid evidence supporting either the association of life-history traits, or the survival cost of fecundity in birds, suggests that the following explanation regarding life-history evolution in the oystercatchers is the most parsimonious one. H. palliatus and H. ostralegus evolved to exploit relatively unpredictable environments and are, as a result, more adaptable. These species invaded numerous environments worldwide. In predictable, colonizing situations their clutch-size is affected by environmental predictability acting on the food supply available to the young. H. ater and H. moquini lay only two eggs in predictable environments due to a combination of past and present selection for larger body size and against larger clutches. Selection for these traits probably resulted from a combination of

factors partly associated with their relatively predictable environments, but the differences in clutch size between the pied and black forms living in sympatry have to be attributable to differences in phylogenetic histories rather than environmental predictability or food supply.

SUMMARY

Reproductive strategies of two species of oystercatchers were studied from 1981 to 1983. Details of the breeding chronology were studied for the American Oystercatcher (Haematopus p. palliatus) in coastal Virginia, U. S. A.. Another subspecies of the American Oystercatcher, H. p. durnfordi, and the sympatric Blackish Oystercatcher H. ater were studied briefly in 1981 and for two months in Argentina in the austral summer of 1982. Some nesting synchrony occurred at several locations in the study area in Virginia in each year. Social stimulation was proposed as one factor which might enhance nesting synchrony. The repeatability estimate for clutch initiation date of known females laying in successive years was high (73%) and demonstrated that females tended to lay at the same time each year. Clutch size in the population of American Oystercatchers in Virginia followed the same pattern in each year of the study. The modal clutch size in first clutches was three eggs, but replacement clutches usually contained two eggs. Egg-size ordering occurs in American Oystercatchers in Virginia. The first egg is smaller than the second egg, but about equal in volume to the third egg in three-egg clutches, and smaller than the second egg in two-egg clutches. The larger second egg may be a result of higher risks of loss for first and third-laid eggs. The egg-size ordering entrains a sibling social hierarchy among the brood that allows for brood reduction in the case of food shortages. It also promotes a more efficient distribution of food because less of the parents' and chicks' energy is wasted during sibling

competition.

The chicks of the American Oystercatcher require extensive parental care. As a result the sex roles in the adults are highly complementary. Males and females expend equal time and energy throughout the breeding season, despite the additional energetic demands of egg-laying by the females. The sex roles are indistinguishable during the pre-laying period. During laying, males chase conspecifics more than do females and this presumably functions to prevent the male from being cuckolded. Consequently cuckoldry appears to be rare in oystercatchers. During incubation the sex roles diverge considerably with females performing most of the incubation duties, and it is energetically less costly for females to do so. During chick-rearing males take more foraging trips to provision the young, wait longer between each trip and take longer trips than females. However, there is no basis for believing that either sex is defaulting or cheating on the frequency of foraging trips. The length of time between trips for both sexes is relatively constant regardless of which sex took the previous trip. The extensive complementarity between the sexes is related to the required parental care for successful rearing of the young and the probability of maintaining the same pair bond in future breeding attempts.

World-wide, oystercatchers exhibit modal clutches of two, or three eggs. H. ater never lays three eggs, although it is sympatric with H. p. durnfordi which lays three eggs about one-third of the time. These two species were contrasted with the subspecies H. p. palliatus in Virginia. The climate experienced by the birds, their behaviour and the habitats they live in were found to be more predictable in Argentina

than in Virginia. Of the three taxa, H. p. palliatus fed the least during the pre-laying period but the most during chick-rearing. H. ater and H. p. durnfordi fed equally in Argentina during pre-laying and probably the same amount during chick-rearing. It is proposed that food supplies for the young account for the lower average clutch size of H. p. durnfordi when compared with H. p. palliatus. Since H. p. durnfordi continues to lay three eggs in a predictable environment predictability alone probably does not account for differences in life-history traits between H. p. durnfordi and H. ater. Differences in clutch size probably resulted from a combination of past and ongoing selection in H. ater for small clutches. Factors affecting clutch size in this species may be related to environmental predictability but also nest-site availability and density-dependent mortality. Species of oystercatchers that lay only two eggs are non-migratory, have restricted nest-site selection, feed on rocky inter-tidal areas and have limited colonizing abilities (e.g. H. bachmani, H. ater, H. moquini, H. fuliginosis, H. chathamensis).

The two species widely differentiated into subspecies (H. palliatus and H. ostralegus) are usually migratory, sometimes lay four eggs, nest on unstable substrates and feed on variable and inassessible prey. Some H. p. durnfordi lay three eggs and there may be little selection against those birds which do lay three. However, this subspecies probably rarely raises three young.

GLOSSARY

Cooperative behaviour. - Individuals engaged in social behaviour in any sized group where the behaviour results in an approximately equal contribution to the fitness of each member of the group.

Predictability. - The degree to which an animal can foretell future conditions.

Social stimulation. - An increased readiness to perform an activity as a result of the presence of conspecifics.

Lack's hypothesis. - The number of eggs in a clutch has been evolved to correspond with that from which on average, the most young are raised.

For species which feed their young the limit is set by the amount of food which the parents can bring their young.

For species which do not feed their young the limit is set by the average amount of food available to the laying female, modified by the size of the egg.

r- and K-selection. -

r-selection is selection for maximum population growth in uncrowded populations.

K-selection is selection for competitive ability in crowded populations.

Life-history strategy. - A set of life-history traits (e.g., age at maturity, clutch size, egg-size) which maximize lifetime fitness.

Reproductive output. - Operationally defined here as the number of eggs produced by the laying female.

Reproductive effort. - The amount of energy put into reproduction, measured in any unit of energy (e.g., kj). The sources of energy expenditure include all costs for courtship, laying, incubating and raising young.

Reproductive value. - The mean amount of future reproductive success fo individuals of that age and sex in the population.

Reproductive cost. - Any activity which results in a lower reproductive value.

LITERATURE CITED

Abrahamson, W. G. and M. Gadgil. 1973. Growth form and reproduc effort in goldenrods. (Solidago, Compositae). Amer. Natur 651-661.

Alcock, J. 1975. Animal behavior: an evolutionary approach. Sin Sunderland, Mass.

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

Allan, J. D. 1984. Life-history variation in a freshwater copep dence from population crosses. Evolution 38: 280-291.

Altmann, J. 1974. Observational study of behaviour: sampling me Behaviour 49: 227-267.

A. O. U. 1983. Checklist of North American Birds. Sixth Ed. Am Ornithologists' Union.

Aschoff, J and H. Pohl. 1970. Rhythmic variations in energy met Federation Proceedings 29: 1541-1552.

Ashkenazie, S. and U. N. Safriel. 1979. Time energy budget of t palmated Sandpiper (Calidris pusilla) at Barrow, Alaska. E 60: 783-799.

Axelrod, R. and Hamilton, W.D. 1981. The evolution of cooperation. Science 211: 1390-1396.

Bader, R. S. and W. H. Lehmann. 1965. Phenotypic and genotypic variation in odontometric traits of the House Mouse. Amer. Midl. Nat. 74: 28-38.

Baker, A. J. 1973. Distribution and numbers of New Zealand Oystercatchers. Notornis 20: 128-144.

Baker, A. J. 1974. Ecological and behavioural evidence for the systematic status of New Zealand Oystercatchers (Charadriiformes: Haematopodidae) Life Sci. Contr., Royal Ontario Museum 96.

Baker, A. J. 1977. Multivariate assessment of the phenetic affinities of Australasian Oystercatchers (Aves: Charadriiformes). Bijdr. Tot. Dierk. 47: 156-164.

Bannerman, D. A. 1961. Birds of the British Isles. Oliver and Boyd, London, England.

Barclay, H. J. and P. T. Gregory. 1981. An experimental test of models predicting life-history characteristics. Amer. Natur. 117: 944-961.

Batschelet, E. 1981. Circular statistics in biology. Mathematics in Biology series. Academic Press, London.

Bergmann, M. 1984. Life history adaptation to demographic regime in laboratory-cultured Tisbe furcata (Copepoda, Harpacticoida). Evolution 38: 292-299.

Bishop, Y.M.M., S.E. Fienberg, and P.W. Holland. 1975. Discrete multivariate analysis. Theory and Practice. Cambridge, Mass. MIT Press.

Blake, E. R. 1977. Manual of neotropical birds. Vol. 1. Univ. of Chicago Press, Chicago.

Box, G. E. P. and G. M. Jenkins. 1970. Time-series analysis: forecasting and control. Holden-Day, San Francisco.

Braun, B.M. and G.L. Hunt, Jr. 1983. Brood reduction in Black-legged Kittiwakes. Auk 100: 469-476.

Briggs, K. 1984. The breeding ecology of coastal and inland Oystercatchers in north Lancashire. Bird Study 31: 141-147.

Brown, K. M. 1983. Do life history tactics exist at the intraspecific level? Data from freshwater snails. Amer. Natur. 121: 871-879.

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

Cairns, W.E. 1977. Breeding biology and behavior of the Piping Plover (ICharadrius melodus) in southern Nova Scotia. Unpublished M. Sc. thesis. Dalhousie Univ., Halifax, Nova Scotia.

Calder, W. A. III. 1974. Consequences of body size for avian energetics. R. A. Paynter (ed.). Nuttall Ornithol. Club. Cambridge, Massachusetts.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge Univ. Press, Cambridge, England.

Clark, A.B. and D.S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. Quart. Rev. Biol. 56: 253-277.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174-184.

Cody, M. L. 1971. Ecological aspects of reproduction. In: Avian Biology. Farner, D. and J. King (eds.). Academic Press, New York. pp. 462-512.

Colwell, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55: 1148-1153.

Constantz, G. D. 1979. Life history patterns of a live bearing fish in contrasting environments. Oecologia 40: 189-201.

Cooley, W. W. and P. R. Lohnes. 1971. Multivariate data analysis. Wiley and Sons, New York.

Coulson, J. C. 1963. Egg size and shape in the Kittiwake (Rissa tridactlya) and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140: 211-227.

Coulson, J. C. 1966. The influence of the pair bond and age on the breeding biology of the kittiwake gull (Rissa tridactyla). J. Anim. Ecol. 35: 269-279.

Coulson, J. C. and J. Horobin. 1976. The influence of age on the breeding biology and survival of the Arctic Tern Sterna paradisaea. J. Zool. Lond. 178: 247-260.

Cramp, S. 1983. Handbook of the birds of Europe, the Middle East and North Africa. Oxford University Press, New York.

Croze, H. 1970. Searching range in carrion crows. Hunting strategy in a predator and some anti-predator devices in camouflaged prey. Zietschrift Tierpsycholgie Bieheft 5: 1-86.

Crump, M. L. 1981. Variation in propagule size as a function of environmental uncertainty for tree frogs. Amer. Natur. 117: 724-737.

Custer, T. W. and F. A. Pitelka. 1972. Time-activity patterns and energy budget of nesting Lapland longspurs near Barrow, Alaska. Proc. 1972 Tundra Biome Symposium, Lake Wilderness Center, University of Washington.

Davis, J.W.F. 1975. Age, egg size and breeding success in the Herring Gull Larus argentatus. Ibis 117: 460-473.

Dawkins, R. 1976. The selfish gene. Oxford University Press, New York.

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

De Steven, D. 1980. Clutch size, breeding success, and parental survival in the tree swallow (Iridoprocne bicolor). Evolution 34: 278-291.

Drent, R., G.F. Van Tets, E. Tompa, and K. Vermeer. 1964. The breeding birds of Mandarte Island, British Columbia. Can. Field-natur. 78:

208-263

Falconer, D.S. 1981. Introduction to quantitative genetics. 2nd ed. London

Fienberg, S.E. 1970. The analysis of multidimensional contingency tables. Ecology 51: 419-433.

Findlay, C.S. and F. Cooke. 1982. Breeding synchrony in the Lesser Snow Goose (Anser caerulescens caerulescens). I. Genetic and environmental components of hatch date variability and their effects on hatch synchrony. Evolution 36: 342-351.

Fisher, R. A. 1958. The genetical theory of natural selection, 2nd. ed. Dover Publications, New York.

Gadgil, M. and O. T. Sobrig. 1972. The concept of r and K selection: evidence from wild flowers and some theoretical considerations. Amer. Natur. 106: 14-31.

Gaines, M. S., K. J. Vogt, J. L. Hamrick and J. Caldwell. 1974. Reproductive stategies and growth patterns in sunflowers (Helianthus). Amer. Natur. 108: 889-894.

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

Gochfeld, M. 1977. Intraclutch egg variation: the uniqueness of the Common Tern's third egg. Bird Banding 48: 325-332.

Grant, P.R. 1982. Variation in the size and shape of Darwin's finch eggs. Auk 99: 15-23.

Graves, J., A. Whiten, and P. Henzi. 1984. Why does the herring gull lay three eggs? Anim. Beh. 32: 798-805.

Groves, S. 1982. Aspects of foraging in Black Oystercatchers (Aves: Haematopodidae). Unpublished Ph. D. thesis. Univ. of British Columbia. Vancouver, Brit. Columbia. 122 p.

Groves, S. 1984. Chick growth, sibling rivalry, and chick production in American Black Oystercatchers. Auk 101: 525-531.

Hahn, D.C. 1981. Asynchronous hatching in the Laughing Gull: Cutting losses and reducing rivalry. Anim. Behav. 29: 421-427.

Hamilton, W. D.1964. The genetical evolution of social behaviour: I,II. J. Theor. Biol. 7: 1-52.

Harder, L. D. 1980. Winter use of montane forests by porcupines in southwestern Alberta: preferences, density effects, and temporal changes. Can. J. Zool. 58: 13-19.

Hart, J. S. and M. Berger. 1972. Energetics, water economy and temperature regulation during flight. Proc. XV Intern. Ornithol. Cong. (The Hague), p. 189-199.

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. 1973. The distribution and taxonomy of oystercatchers. Notornis 20: 102-112.

Hockey, P. A. R. 1983a. The distribution, population size, movements and conservation of the African Black Oystercatcher (Haematopus moquini). Biol. Conserv. 25: 233-262.

Hockey, P. A. R. 1983b. Ecology of the African Black Oystercatcher Haematopus moquini. Unpublished Ph. D. thesis. University of Cape Town, Cape Town, South Africa. 409 p.

Hockey, P. A. R. 1984. Growth and energetics of the African Black Oystercatcher Haematopus moquini. Ardea 72: 111-117.

Hogstedt, G. 1981. Should there be a positive or negative correlation between survival of adults in a bird population and their clutch size? Am. Natur. 118: 568-571.

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

Holmes, R. T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (Calidris alpina). Condor 73: 93-99.

Holmes, R. T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (Calidris mauri) in subarctic Alaska. Am. Midl. Natur. 87: 472-491.

Howe, H. F. 1976. Egg size, hatching asynchrony, sex and brood reduction in the Common Grackle. Ecology 57: 1195-1207.

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

Jehl, J. R. Jr. 1968. Relationships in the Charadrii (shorebirds) : a taxonomic study based on color patterns of the downy young. San Diego Soc. Nat. Hist. Memoir 3, San Diego.

Jehl, J. R., Jr. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bull. 85: 115-147.

Jehl, J. R., M. A. E. Rumboll, and J. P. Winter. 1973. Winter bird populations of Golfo San Jose, Argentina. Bull. Brit. Orn. Cl. 93: 56-63.

Kaplan, R. H. and W. S. Cooper. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin-flipping" principle. Amer. Natur. 123: 393-410.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. In: Avian energetics. R. A. Paynter, Jr. (ed.) Publ. of the Nuttall Ornith. Club 15: 4-70.

Knowlton, N. 1979. Reproductive synchrony, parental investment, and the evolutionary dynamics of sexual selection. Anim. Beh. 27: 1022-1033.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Larson, S. 1957. The suborder Charadrii in Arctic and Boreal areas during the Tertiary and Pleistcene. Acta Vertebratica 1: 1-84.

Law, R., A. D. Bradshaw and P. D. Putwain. 1977. Life-history variation in Poa annua. Evolution 31: 233-246.

Legand, M. 1958. Variations diurnes du zooplancton autour de la Nouvell-Caledonie. O.R.S.T.O.M., Inst. fr. Oceanie Section Oceanogr., Rapp. Sci. 6: 1-42.

Lenington, S. and T. Mace. 1975. Mate fidelity and nesting-site tenacity in the Killdeer. Auk 92: 149-151.

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

Leutonegger, W. 1979. Evolution of the litter size in primates. Amer. Natur. 114: 525-531.

Luckinbill, L. S. 1984. An experimental analysis of life history theory. Ecology 65: 1170-1184.

Lundberg, C., and R.A. Väisänen. 1979. Selective correlation of egg size with chick mortality in the Black- headed Gull (Larus ridibundus). Condor 81: 146-156.

MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. Amer. Natur. 100: 603-609.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey.

MacArthur, J. W. 1975. Environmental fluctuations and species diversity. In: Ecology and evolution of communities. Cody, M. L. and J. M. Diamond (eds). Belknap Press, Cambridge, Mass.

Maclean, G. L. 1972. Clutch size and evolution in the Charadrii. Auk 89: 299-324.

Makkink, G. F. 1942. Contribution to the knowledge of the behaviour of the Oyster-Catcher. (Haematopus ostralegus L.). Ardea 31: 22-74.

Mandelbrot, B. B. 1983. The fractal geometry of nature. Freeman and Co., New York.

Maurmeyer, E. 1981. Geology of the coastal bays. In: Proc. of conference on the coastal bays of Maryland and Virginia. Committee to Preserve Assateague Island, Inc. 110 pp.

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

May, R. M. 1976. Patterns in multi-species communities. In: May, R. M. (ed.). Theoretical ecology: principles and applications. Saunders Co., Philadelphia.

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

Menge, B. A. 1974. Effect of wave action and competition on brooding and reproductive effort in the sea star Leptasterias hexactis. Ecology 55: 84-93.

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

Miller, E. H. 1979. Egg size in the Least Sandpiper Calidris minutilla on Sable Island, Nova Scotia, Canada. Ornis Scandinavica. 10: 10-16.

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

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

Mills, J.A. 1979. Factors affecting the egg size of Red-billed Gulls Larus novaehollandiae scopulinus. Ibis 121: 53-67.

Mills, J.A. and J. P Ryder. 1979. Trap for capturing shore and seabirds. Bird-banding 50: 121-123.

Mock, D. W. 1979. Display repertoire shifts and extramarital courtship in herons. Behaviour 69: 57-71.

Montevecchi, W. and J. Porter. 1980. Parental care and related behavior before fledging in northern gannets (Morus bassanus) with reference to other marine birds. In: Behavior of marine animals. Vol. IV. Marine birds. (Burger, J., Olla, B., and Winn, J. eds.).- Plenum, New York. p. 323-366.

Montevecchi, W. A., R. E. Ricklefs, I. R. Kirkham and D. Gabaldon. 1984. Growth energetics of nestling Northern Gannets (Sula bassanus). Auk 101: 334-341.

Mosimann, J.E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. J. Amer. Stat. Assoc. 65: 930-945.

Mosimann, J. E. and F.C. James. 1979. New statistical methods for allometry with applications to Florida Red-winged Blackbirds. Evolution 33: 444-459.

Moss, R. and A. Watson. 1982. Heritability of egg size, hatch weight, body weight, and viability in Red Grouse (Lagopus lagopus scoticus). Auk 99: 683-686.

Nethersole-Thompson, D. 1951. The greenshank. Collins Press, London, England.

Nettleship, D. N. 1973. Breeding ecology of turnstones Arenaria interpres at Hazen Camp, Ellesmere Island, N.W.T. Ibis 115: 202-217.

Niebuhr, V. 1983. Feeding strategies and incubation behaviour of wild herring gulls: and experiment using operant feeding boxes. Anim. Behav. 31: 708-717.

Nisbet, I.C.T. and M.E. Cohen. 1975. Asynchronous hatching in Common and Roseate Terns, Sterna hirundo and S. dougallii. Ibis 117: 374-379.

Nisbet, I.C.T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate terns, Sterna hirundo and S. dougallii. Ibis 120: 207-215.

Nol, E. and A. Lambert. 1984. Comparision of Killdeers breeding in mainland and peninsular sites in southern Ontario. Can. Field-Natur. 98: 7-11.

Norton, D.W. 1970. Thermal regime of nests and bioenergetics of chick growth in the Dunlin (Calidris alpina) at Barrow, Alaska. Unpubl. M.S. thesis. Univ. of Alaska, College.

O'Connor, R.J. and R.A. Brown. 1977. Prey depletion and foraging strategy in the Oystercatcher Haematopus ostralegus. Oecologia 27: 75-92.

Ojanen, M. M. Orell and R.A. Vaisanen. 1979. Role of heredity in egg size variation in the Great Tit Parus major and the Pied Flycatcher Ficedula hypoleuca. Ornis Scandinavica. 10: 22-28

Oliver, W. R. B. 1955. New Zealand birds. A. H. and A. W. Reed. Wellington, New Zealand.

Orians, G. H. 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31: 285-312.

Parry, G. D. 1981. The meanings of r- and K-Selection. Oecologia 48: 260-264.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (Larus argentatus). Nature 228: 1221-1222.

Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull Larus argentatus. Ibis 117: 517-520

Parsons, J. 1975. Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success. J. Anim. Ecol. 44: 553-573.

Pianka, E. R. 1970. On r and K selection. Amer. Natur. 104: 592-597.

Pielou, E. C. 1975. Ecological diversity. Wiley Interscience Press, New York.

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.

Richardson, B. J. 1975. r and K selection in Kangaroos. Nature 255: 323-324.

Ricklefs, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67: 505-510.

Ricklefs, R. E. 1974. Energetics of reproduction in birds In: Avian energetics. R. A. Paynter (ed.). Nuttall Ornithol. Club No. 15.

Safriel, U. 1967. Population and food study of the Oystercatcher. Ph. D. thesis. Oxford Univ., Oxford, England.

Safriel, U. N. 1975. On the significance of clutch size in nidifugous birds. Ecology 56: 703-708.

Safriel, U. N. 1981. Social hierarchy among siblings in broods of the Oystercatcher Haematopus ostralegus. Behav. Ecol. Sociobiol. 9: 59-63.

Safriel, U. N., M. P. Harris, M. de L. Brooke, and C. K. Britton. 1984. Survival of breeding oystercatchers Haematopus ostralegus. J. Anim. Ecol. 53: 867-877.

Schwartz, S. S. 1984. Life history strategies in Daphnia: a review and predictions. Oikos 42: 114-122.

Slater, P. 1971. A field guide to Australian birds. Livingston, Wynnewood, Pennsylvania.

Smith, J. N. M. 1974a. The food searching behaviour of two European thrushes. I. Description and analysis of search paths. Behaviour 48: 276-302.

Smith, J. N. M. 1974b. The food searching behaviour of two European thrushes. II. The adaptiveness of the search patterns. Behaviour 49: 1-61.

Smith, J. N. M. 1981. Does high fecundity reduce survival in song sparrows? Evolution 35:1142-1148.

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

Sokal, R.R. and F.J. Rohlf. 1981. Biometry, 2nd. ed. San Francisco. Freeman and Co.

Spence, I. 1979. Multidimensional scaling. In: Quantitative ethology. Colgan, P. W. (ed.) Wiley and Sons, New York.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.

Stearns, S. C. 1980. A new view of life-history evolution. Oikos 35: 266-281.

Stearns, S. C. 1983a. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos 41: 173-287.

Stearns, S. C. 1983b. A natural experiment in life-history evolution: field data on the introduction of mosquitofish (Gambusia affinis) to Hawaii. Evolution 37: 601-617.

Stearns, S. C. 1983c. The genetic basis of differences in life-history traits among six populations of mosquitofish (Gambusia affinis) that shared ancestors in 1905. Evolution 37: 618-627.

Stearns, S. C. 1984. The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. Amer. Natur. 123: 56-72.

Stubbs, M. 1978. Density dependence in the life-cycles of animals and its importance in K and r strategies. J. Anim. Ecol. 46: 677-688.

Tamarin, R. H. 1978. Dispersal, population regulation and K selection in field mice. Amer. Natur. 112: 545-555.

Tatsuoka, M. M. 1971. Multivariate analysis. Techniques for educational and psychological research. Wiley and Sons, New York.

Taylor, C. E. and C. Condra. 1980. r- and K- selection in Drosophila pseudoobscura. Evolution 34: 1183-1193.

Tinbergen, N., M. Impekoven and D. Franck. 1967. An experiment on spacing out as a defence against predation. Behaviour 28: 307-321.

Tinkle, D. W., H. M. Wilbur and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24: 55-74.

Trivers, R. L. 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man. (Campell, B. ed.). Aldine, Chicago. p. 136-179.

Tuomi, J., T. Hakala and E. Haukioja. 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. Amer. Zool. 23:25-34.

Vaisanen, R.A. 1969. Evolution of the Ringed Plover (Charadrius hiaticula L.) during the last hundred years in Europe. A new computer method based on egg dimension. Ann. Acad. Sci. Fenn. A. IV 149: 1-90.

Vaisanen, R.A., O. Hilden, M. Soikkeli, and S. Vuolanto. 1972. Egg dimension variation in five wader species: the role of heredity. Ornis Fenn. 40: 25-44.

Van Noordwijk, A.J., L.C.P.Keizer, J.H. Van Balen and W. Scharloo. 1981. Genetic variation in egg dimensions in natural populations of

the Great Tit. Genetica 55: 221-232.

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

Warham, J. 1974. The Fiordland Crested Penguin Eudyptes pachyrhynchus. Ibis 116: 1-23.

Webster, J. D. 1942. Notes on the growth and plumages of the Black Oystercatcher. Condor 44: 205-211.

Welty, J. C. 1975. The Life of Birds. 2nd Ed.- Saunders Co. Philadelphia.

Williams, G. C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. Amer. Natur. 100: 687-690.

Willson, M. F. and E. R. Pianka. 1963. Sexual selection, sex ratio and mating systems. Amer. Natur. 97:405-407.

Wood, R. W. 1975. The birds of the Falkland Islands. Anthony Nelson, New York.

Zach, R. 1977. Foraging behaviour of the ovenbird (Aves: Parulidae) in a patchy environment. Unpublished Ph D thesis. Univ. of Toronto, Toronto.