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THE BIOLOGY AND SYSTEMATIC RELATIONSHIPS OF CROWNED, BLACKWINGED AND LESSER BLACKWINGED PLOVERS

by

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PREFACE

The experimental work described in this thesis was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from January 1985 to July 1987, under the supervision of Professor Gordon L. Maclean.

These studies represent original work by the author and have not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.

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Most of all, I wish to express my gratitude to my parents for stimulating my interest in birds, for supporting and encouraging me throughout my studies, for guiding me without pushing me and for their love.

ABSTRACT

The biology of Crowned, Blackwinged and Lesser Blackwinged Plovers was compared with particular reference to breeding biology, feeding ecology and habitat preference. Crowned and Blackwinged Plovers coexisted in mixed flocks in grasslands which aided predator detection and defence against predators. Lesser Blackwinged Plovers were opportunistic in their use of habitat and were found in habitats ranging from the muddy edges of pans to woodlands. Body size was found to have an important effect on the breeding biology of these birds, affecting incubation behaviour and reproductive pattern. The behaviour of Lesser Blackwinged Plovers differed considerably from that of Crowned and Blackwinged Plovers. Crowned and Blackwinged Plovers appear to constitute a superspecies on account of their behavioural and morphological similarities while the Lesser Blackwinged Plover is possibly closely related to the ancestral stock of the genus *Vanellus*.

INTRODUCTION

Vanelline plovers or lapwings (*Vanellinae: Charadriidae: Charadriiformes*) are found on all continents except North America and Antarctica (Fig. 1). They are a diverse group of birds as far as the colour and pattern of the body plumage are concerned, although they have a common tail and wing pattern. The tail is white with a broad black subterminal band. The primaries are black and most species have a broad white wing stripe that begins on the greater primary-coverts and extends diagonally across the secondary coverts and the secondaries. Many species possess facial wattles and wing spurs. Vanelline plovers are all inland birds, found on dry grasslands, open woodlands, marshes or the edges of streams and rivers.

Crowned Plovers *Vanellus coronatus*, Blackwinged Plovers *V. melanopterus* and Lesser Blackwinged Plovers *V. lugubris* are medium-sized birds (22-30 cm tall). These three species formerly constituted the genus *Stephanibyx* (Peters 1934) until Bock (1958) grouped all members of the Vanellinae into the single genus *Vanellus*. Unlike most other members of the order Charadriiformes, Crowned, Blackwinged and Lesser Blackwinged Plovers do not usually occupy habitats associated with water, but are most commonly found in open grasslands and, in the case of Lesser Blackwinged Plovers, open woodlands.

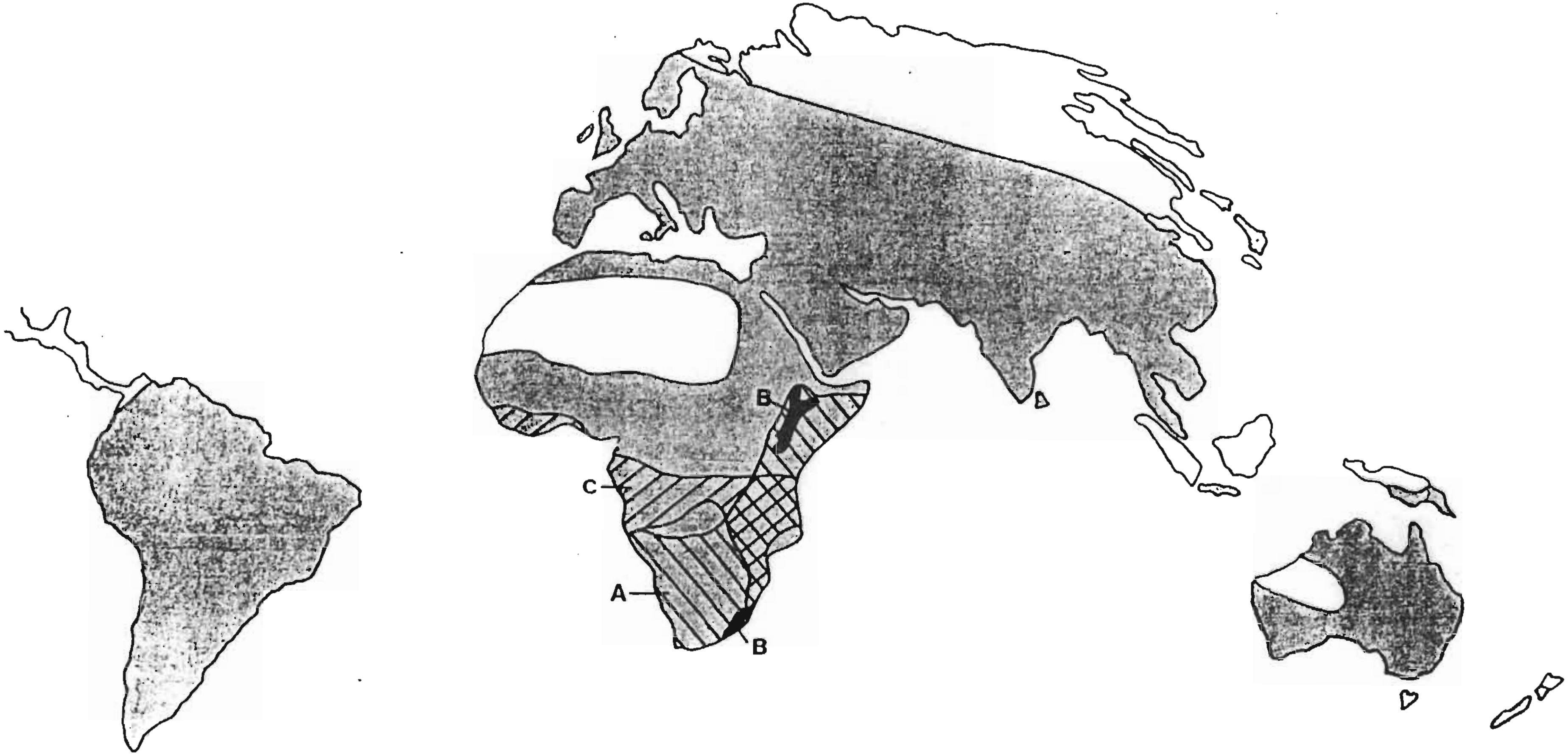


Fig. 1. Distribution of the Vanellinae (shading), with particular reference to the distribution of Crowned Plovers (A), Blackwinged Plovers (B) and Lesser Blackwinged Plovers (c), after Hayman <u>et</u> <u>al.</u> 1986.

The study species

Detailed descriptions of the three study species are available in Clancey (1964), Johnsgard (1981) and Maclean (1985). The following are brief summaries of the birds' appearance:

a) Crowned Plover (Fig. 2a and b)

The Crowned Plover *Vanellus coronatus* (Boddaert 1783) is found widely in southern and eastern Africa (Fig. 1) in areas of short, overgrazed or burnt grass. Adults of both sexes are light brown on the upperparts, chest and breast with a black line separating these parts from the white belly. The forehead and crown are black with a white coronal circlet. The undertail and underwing coverts are white and the tail is white with a broad black subterminal band. The primary feathers are black, the secondaries white with black tips. The legs are red as is the base of the bill, which has a black tip.

In spite of their wide distribution and relative abundance, the biology of Crowned Plovers has not been extensively studied. Knowledge of the biology of this species is limited to natural-history studies by Skead (1955) and Ade (1979).

b) Blackwinged Plover (Fig. 2c and d)

The Blackwinged Plover *Vanellus melanopterus* (Cretzschmar 1829)

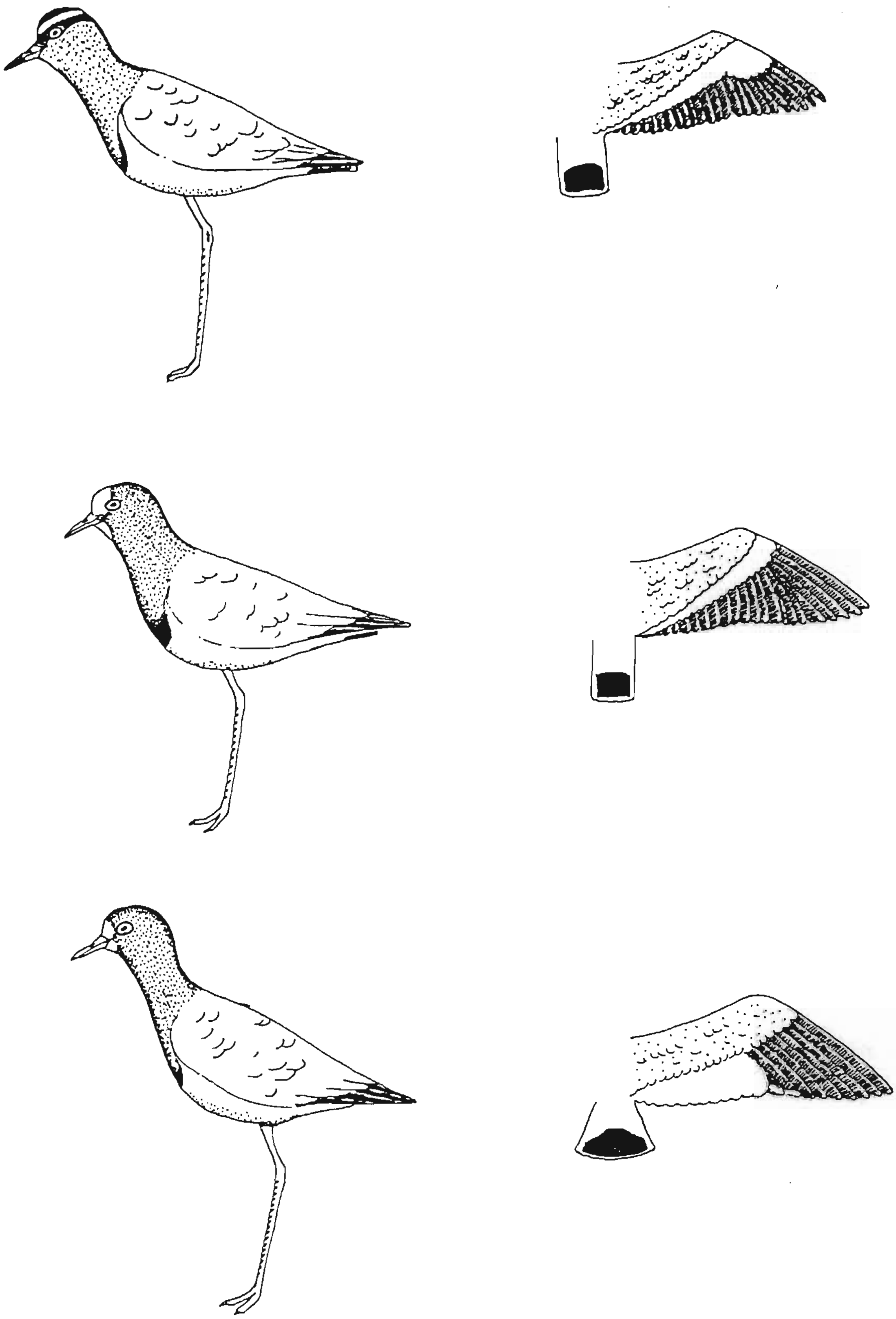


Fig. 2. Line drawings of the study species. (a) Crowned Plover. (b) Dorsal view of Crowned Plover wing and tail pattern. (c) Blackwinged Plover. (d) Dorsal view of Blackwinged Plover wing and tail pattern. (e) Lesser Blackwinged Plover. (f) Dorsal view of Lesser Blackwinged Plover wing and tail pattern.

has a disjunct distribution, occurring in northeastern Africa (eastern Sudan, Ethiopia and Kenya) and in southern Africa (southeastern Transvaal, eastern Swaziland, Natal and eastern Cape) (Fig. 1) in short or burnt grasslands. Adults of both sexes have brown upperparts and a grey head, throat and chest. The chest is separated from the white belly by a black band. The forehead is white while the lores and chin are a lighter grey colour than the rest of the head and neck. The undertail and underwing coverts are white, as is the tail which has a broad black subterminal band. The primaries are black, the secondaries white with black tips. The legs are brown with a red tinge. The bill is brown with a black tip.

Knowledge of the biology of Blackwinged Plovers is limited to behavioural observations by Maclean (1972) and a natural history study by Butcher (1984, MS).

c) Lesser Blackwinged Plover (Fig. 2e and f)

The Lesser Blackwinged Plover *Vanellus lugubris* (Lesson 1826) occurs across equatorial Africa and in southeastern Africa as far south as the southeastern Transvaal and northern Natal, South Africa (Fig. 1) in short or burnt grass. Adults of both sexes have brown upperparts with an iridescent green tinge to the mantle, wing coverts and scapulars. The chest is separated from the white belly by a black band. The forehead is brown with a small white patch extending from the bill to just in front of the eyes. The underwing and undertail coverts are white, as is the tail which has a broad black subterminal band. The primaries are black while the secondaries are white. The legs are black. The bill is brown with a black tip.

No studies of the biology of this species have been done.

The phylogenetic relationships of Crowned, Blackwinged and Lesser Blackwinged Plovers.

Peters (1934) considered Crowned, Blackwinged and Lesser Blackwinged Plovers to be sufficiently different from other members of the Vanellinae to constitute the genus *Stephanibyx*. Bock (1958) considered Peters' (1934) classification, which separated the 23 species in the Vanellinae into 19 genera, unjustified because of the small morphological variation between species and placed all 23 species in the genus *Vanellus*.

Johnsgard (1981) suggested that the Sociable Plover *V. gregarius* might be the Crowned Plover's nearest relative, while Seebohm (1888) suggested that the Blackwinged Plover might be more closely related to the Crowned Plover. Glutz von Blotzheim *et al.* (1975), on the other hand, proposed that the Crowned Plover possibly belonged to the genus *Chettusia*, along with *V. gregarius*, *V. leucurus*, *V. crassirostris* and *V. melanopterus*.

Blackwinged and Lesser Blackwinged Plovers may constitute a superspecies (Snow 1978; Johnsgard 1981). Seebohm (1888) considered the Lesser Blackwinged Plover to be the West African representative of the Blackwinged Plover.

Although there is some debate about the phylogenetic relationships of species within the subfamily Vanellinae, it appears that there is consensus among systematists that Crowned, Blackwinged and Lesser Blackwinged Plovers are closely related members of a subgroup of vanelline plovers including, at most, three other species.

Aims of this study

Crowned, Blackwinged and Lesser Blackwinged Plovers were chosen for study because :

a) they constitute an evolutionary complex of species (Bock 1958)

b) direct comparisons of different aspects of the biology of the species could be made because of the similarity of the habitats occupied.

c) the behavioural displays of these species are relatively elaborate and easily observed, facilitating interpretation of possible cause and effect.

d) Crowned and Blackwinged Plovers frequently occur in mixed-species flocks (Skead 1955; Maclean 1985), contrary to the predictions of community theory (Diamond 1975), suggesting that a study of their feeding ecology would be useful to determine the mechanisms that facilitate coexistence.

e) all three species nest in the open without shade for the incubating bird, making these species suitable for a study of incubation under severe conditions. Because Crowned and Blackwinged Plovers are of a similar size, while Lesser Blackwinged Plovers are about one-third smaller (see Appendix), a comparison of incubatory adaptations between species could be made to determine whether these adaptations are affected by body size or by some other variable.

This study was designed to investigate the biology of each of the three study species bearing the above five points in mind. In the light of their similarity in size, habitat preference and phylogeny, I emphasized comparison of the various aspects of their biology. In addition, the interactions of these plovers with other species in the same habitat were studied to determine the importance and status of the plovers in their ecosystems.

The discovery of substantial differences in the behaviour of the Lesser Blackwinged Plover relative to the other two species led to another facet of this study, namely a study of the phylogeny of these species by means of a comparison of their morphologies and behaviour. In order to determine whether the differences in behaviour and morphology between these species were significant, comparison was made with two other vanelline plovers, namely the Blacksmith Plover _Vanellus armatus_ and the Wattled Plover _V. senegallus_.

Study sites

From January 1985 to June 1987, Crowned and Blackwinged Plovers were studied in the vicinity of Pietermaritzburg (29°30'S 30°30'E), Natal, South Africa (Fig. 3). The five study areas chosen (Chapter 2, Fig. 1) were the major areas used by Crowned and Blackwinged Plovers in the Pietermaritzburg district. Each was about 20 ha in extent and, at the time that the plovers were present on them, consisted of short or burnt grass. The study areas varied in slope from 0-10°.

From September 1985 to December 1986, Crowned and Lesser Blackwinged Plovers were studied in the vicinity of Ndumu (26°30'S 32°45'E), northern Natal (Fig. 3). Two major study areas and five minor study areas were located in Ndumu Game Reserve (Fig. 4), 2 km north of Ndumu. One area (Bunguzane) was a 1-ha clearing in a thicket with a few scattered *Acacia nilotica* trees, while the other (NRC) was a 25-ha open woodland consisting of *A. nigrescens*, *A. nilotica*, *A. tortilis* and *Sclerocarya caffra*. The two above-mentioned study areas were virtually flat, covered by short or burnt grass when used by the plovers, and had no understory vegetation. For a more detailed description of vegetation in Ndumu Game Reserve see De Moor *et al.* (1977). Another study area (Ndumu Estates) was 3 km south of Ndumu (Fig. 4) and was about 40 ha in size and consisted of overgrazed, gently sloping (about 15° slope) grassland previously under cultivation. A small area of Ndumu Estates of about 2 ha

Fig. 3. Areas of study in Natal (marked with an X).

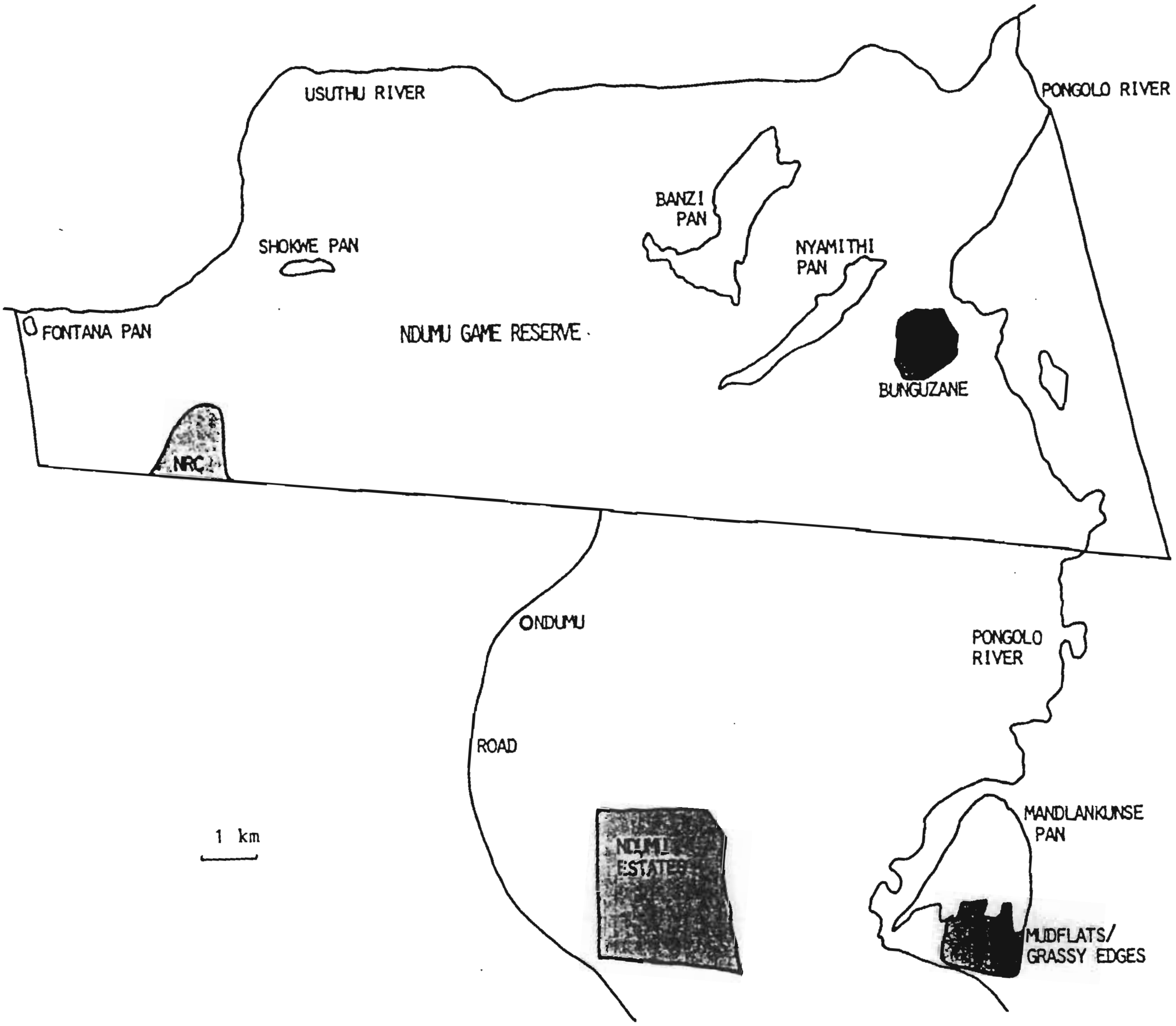


Fig. 4. Schematic diagram of study areas near Ndumu, northern Natal.

consisted of open Acacia nilotica woodland with short grass.

In addition, observations of Crowned, Blackwinged and Lesser Blackwinged Plovers were made opportunistically wherever these plovers were found in Natal. The most important of these sites are shown in Fig. 3.

Chapter 1

HABITAT SELECTION

INTRODUCTION

Detailed knowledge of habitat selection by Crowned, Blackwinged and Lesser Blackwinged Plovers is scanty and scattered through the literature. Crowned Plovers have been recorded in short or burnt grasslands and open woodlands over a wide range of environmental conditions from the coast to the Kalahari desert (Johnsgard 1981) in southern and eastern Africa. Blackwinged Plovers occur in short or burnt highland grasslands at altitudes above 1300 m above sea level in East Africa (Britton 1980), although they have been recorded from highland grasslands and at sea level in South Africa (Cyrus 1982; Maclean 1985). Lesser Blackwinged Plovers have been recorded from grasslands and open woodlands in Natal (Cyrus & Robson 1980), typically near water in east Africa (Britton 1980), in grasslands and woodlands in Rwanda (Van der Weghe & Monfort-Braham 1975) and once from the seashore in Zanzibar (Pakenham 1979). Lesser Blackwinged Plovers are usually found below 800 m a.s.l. (Britton 1980). These three plover species therefore occupy habitats with a considerable degree of overlap between species and a detailed study of the ecological relationships between these species requires an exact knowledge of their habitat selection.

In order to determine the ecological relationships between Crowned, Blackwinged and Lesser Blackwinged Plovers and their ecological relationships with other species, it is necessary to examine the distribution of the species to determine whether there is overlap at this scale and then to examine niche utilization.

The analysis of factors influencing the distribution of a species can be made by comparing the distribution with known environmental variables such as altitude, temperature, rainfall and vegetation. The most comprehensive data on the distribution of these plovers in Natal have been compiled by Cyrus & Robson (1980) for the 10-year period from 1970-1979. These data were lumped over the study period for each quarter-degree square in the province, _i.e._ if a bird was recorded one or more times over the 10-year period in a quarter-degree square it was denoted as present. Since factors such as rainfall, mean annual/monthly temperature or humidity vary from year to year, it was decided that altitude was the only gradient with which a comparison of species distributions could be made, using the data available. Altitude was found to be strongly correlated with temperature in Natal ($\underline{r}$ = -0,87; $p < 0,05$ for mean January temp.; $\underline{r}$ = -0,85; $p < 0,05$ for mean July temp.) but not with rainfall ($\underline{r}$ = -0,479; $p > 0,05$; n.s.). Correlation of species distributions with environmental variables can be used only as a weak inference that environmental gradients govern species distributions because any large-scale natural gradient is likely to contain many variables, both independent and dependent, which influence distribution patterns (Terborgh 1971).

Stuckenberg (1969) suggested that temperature was a causal factor contributing to the formation of faunal assemblages in Africa. Stuckenberg stressed the biological importance of summer months and described a factor called effective temperature, developed by Bailey (1960), to express the relative warmth and duration of the warm period of the year. Effective temperature measures warmth on a temperature scale, specifying temperatures at the beginning and end of the warm period , and implicating the duration of that period. Stuckenberg has shown that a close correlation exists between the distribution of snakes and frogs and effective temperature zones. Stuckenberg has also demonstrated that the mean July isotherm, used by Poynton (1962) to delineate amphibian species' assemblages, is an innaccurate climatic indicator. Likewise, Stuckenberg rejected Bowen's (1933) attempt at a climatic classification based on various parameters of temperature and rainfall, which Bowen suggested were pertinent to bird distribution. The apparent usefulness of effective temperature in delineating species assemblages indicates that it may be useful in describing the distributions of Crowned, Blackwinged and Lesser Blackwinged Plovers, particularly because birds can chose their summer distributions and many species including Blackwinged Plovers (Maclean 1985) are known to migrate to warmer areas in winter.

Vegetation gradients were not considered at all in this study of the distribution of these plover species because of the difficulty in defining vegetation types (*e.g.* should vegetation be separated into forest/woodland/savanna/grassland or *Acacia* woodland/*Sclerocarya caffra* woodland/*Themeda triandra* grassland/*Aristida junciformis* grassland, *etc.* ?). In any case, Crowned, Blackwinged and Lesser Blackwinged Plovers are insectivorous and are thus only indirectly dependent on vegetation as it affects their food supply.

The literature on methods of determining niche use and preferences in animals is vast and contains many contradictory examples proposing the use of one method in preference to another (*e.g.* Dueser & Shugart 1982; Van Horne & Ford 1982; Carnes & Slade 1982; James & McCullough 1985). Multivariate distance measures are widely used and are a major ingredient of the statistical analysis of niche width and niche overlap (Atchley *et al.* 1982, James & McCullough 1985). Many of these methods are concerned with comparing mean niche position rather than the range of niche positions occupied, the latter measure being more important in a comparative study of ecological relationships between species, thus rendering means unsuitable for the purposes of this study. Other pitfalls in the use of multivariate statistics are reviewed by Williams (1983) and James & McCullough (1985). Multivariate distance methods are inappropriate in the case of this study because the habitat and niche differences were obvious where they occurred, so univariate methods were used instead.

Abundance has not been used as an index of habitat preference in this study since it is of dubious value because, for example, is a habitat more important to a species if it is used by two individuals for 100 days, five birds for 40 days or by 20 birds for 10 days ? Surely the only factor of importance is that members of the species use the habitat, regardless of how often ? An advantage in not including indices of abundance in determining habitat preferences of a species is that conclusions are not affected by sample size. An index of abundance is particularly unsuitable in a study of Crowned, Blackwinged and Lesser Blackwinged Plovers because they often feed in large groups and nest in loose colonies (pers. obs.) so that the number of birds in an area may not be directly related to habitat preference but rather to other factors such as the anti-predatory ability of a large group or the chance association of a group of birds in a certain area.

For the above-mentioned reasons, niche selection was determined by considering the entire range of habitats occupied, regardless of the number of individuals present, and by comparing the range of habitats used by the three species to determine the importance of ecological relationships between the species and the potential for these relationships to occur.

MATERIALS AND METHODS

Distributions of Crowned, Blackwinged and Lesser Blackwinged Plovers were analyzed using data from Cyrus & Robson (1980)(Fig. 1.1a, b and c), who divided Natal into quarter-degree squares and denoted the presence/absence of each avian species in Natal for each month of the year over a ten-year period (1970-1979). In order to determine the correlation of the three species with altitude, species preference was computed against altitude. Altitude was grouped into 300-m increments (from sea level), with the exception of 301-900 m which formed a single group because of the undulating nature of the terrain in this altitudinal range (Cyrus & Robson 1980). The measure of preference used was the number of months that a species was recorded in an area corresponding to a 300-m altitudinal group over all quarter-degree squares within the group. This number was computed as a percentage of the total number of months over all quarter-degree squares that the species was recorded in Natal.

The degree of overlap of the distributions of Crowned and Blackwinged Plovers within the range of the Blackwinged Plover (since it has a more restricted distribution) was compared, over all months, using a 2 x 2 contingency analysis (Sokal & Rohlf 1969) of the data of Cyrus & Robson (1980).

Grass height in Crowned and Blackwinged Plover habitats was measured at Ukulinga Research Farm, Pietermaritzburg using the

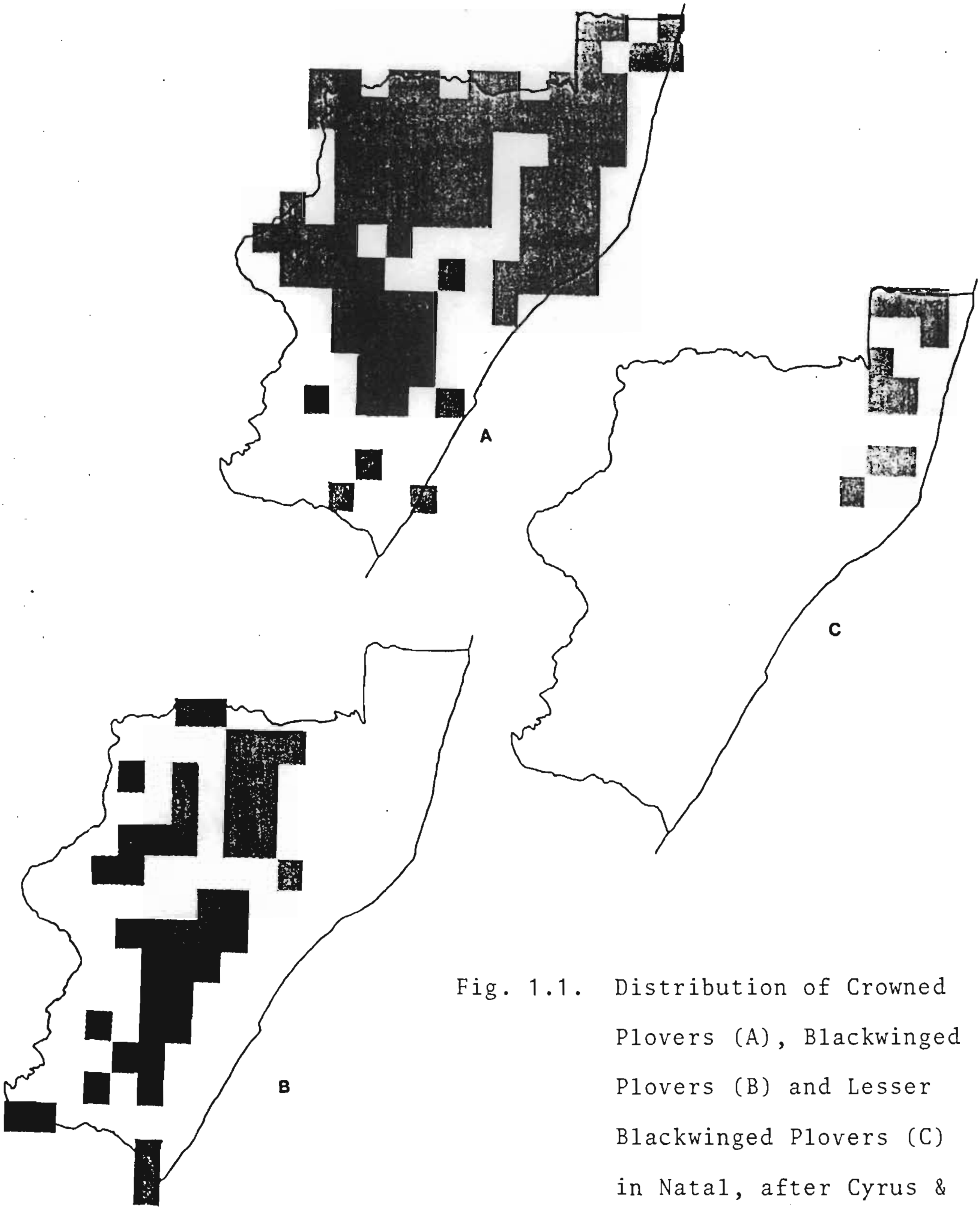


Fig. 1.1. Distribution of Crowned Plovers (A), Blackwinged Plovers (B) and Lesser Blackwinged Plovers (C) in Natal, after Cyrus & Robson (1980).

point-intercept method (Mueller-Dombois & Ellenberg 1974) in 24 50-m x 50-m plots, each with 100% grass density.

The point-centred quarter method (Mueller-Dombois & Ellenberg 1974) was used to determine tree densities in woodlands occupied by Lesser Blackwinged and Crowned Plovers in Ndumu Game Reserve and at Ndumu Estates.

The effective temperature at all sites occupied year-round by Crowned, Blackwinged and Lesser Blackwinged Plovers was computed using data from the weather station nearest the study site (and within that quarter-degree square (Cyrus & Robson 1980)), compiled by the Computing Centre for Water Research at the University of Natal.

The physical structures of woodlands occupied by Crowned and Lesser Blackwinged Plovers were compared using the method of mean character difference (M.C.D.), devised by Cain & Harrison (1958) for systematics studies. Each variable (e.g. stem density of trees, canopy cover, tree height, etc.) was entered into the equation as a mean value and the sum of the differences between each variable was then obtained for each pair of woodlands studied. These mean character difference values were then plotted graphically, using the two-dimensional ordination technique of Bray & Curtis (1957), which is considered to be more accurate than comparable multivariate techniques (Gauch & Whittaker 1973).

RESULTS

Lesser Blackwinged Plovers were recorded only on the northern Natal coastal plain below 300 m. Crowned Plovers were recorded from sea level up to 1500 m (Fig. 1.2) while Blackwinged Plovers were recorded from 300-1800 m, with a distinct preference for the range 900-1500 m. The overlap of the distributions of Crowned and Blackwinged Plovers over all months, within the range of the Blackwinged Plover, was highly significant (χ^2 = 62,98; p <0.001).

Crowned Plovers occupied the widest range of effective temperatures (range = 5,48 °C) with a mean ±S.E. effective temperature of 16,51 ±0,28 °C. Crowned Plovers were found in areas where the effective temperature is >15 °C. Blackwinged Plovers occupied areas with a mean ±S.E. effective temperature of 15,40 ±0,3 °C (range = 1,98 °C) and are usually found between 15 and 16°C effective temperatures. Lesser Blackwinged Plovers were found in areas with a mean ±S.E. effective temperature of 18,37 ±0,18 °C (range = 0,26 °C).

Crowned and Blackwinged Plovers occupied seven plots simultaneously at Ukulinga over the entire trial period of eight weeks. Mean grass height in preferred plots was 4,23 ±0,16 cm. Mean maximum grass height was 5,70 cm while the mean minimum grass height was 2,32 cm. The shortest grass height in unselected plots was 6,24 ±0,35 cm. Crowned and Blackwinged Plovers were

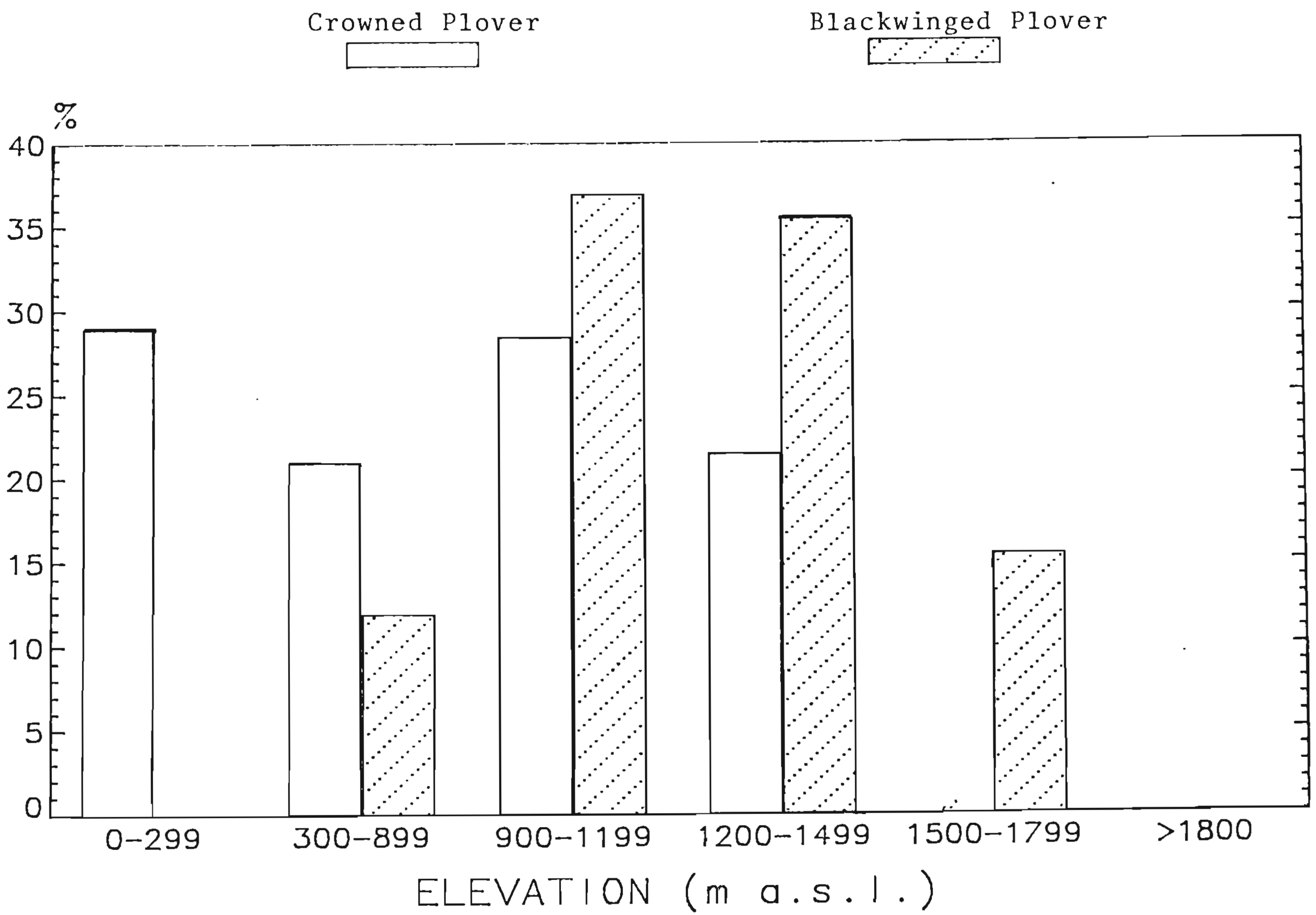


Fig. 1.2. Altitudinal distribution of Crowned and Blackwinged Plovers in Natal. Altitude preference was determined by the number of months in which a species was present in each quarter-degree square (Cyrus & Robson 1980) at a specific range of altitude, computed as a percentage of the total number of months in which the species was recorded in Natal.

found, at sites all over Natal, over the entire range of grass densities from 0%-100%.

Blackwinged Plovers were found only in short or burnt grass areas during the study period. Crowned Plovers were found in short or burnt grass, cultivated fields and in open woodlands with short or burnt grass. Crowned Plovers occupied cultivated fields opportunistically to feed on invertebrates unearthed by ploughing and tilling operations (pers. obs.). Crowned Plovers rarely occupied open woodlands (n = 7 occasions (total of 31 birds), not including the two pairs which nested in these woodlands). The density of trees in the woodland occupied by one nesting pair (the same woodland used by the 31 birds mentioned above) was 0,11 trees per 100 m^2 (canopy cover was not measured because tree density was so low). The woodland that the other pair nested in was the only one of the two also occupied by Lesser Blackwinged Plovers and had a tree density of 1,19 trees per 100 m^2 with a canopy cover of 25,3%.

Lesser Blackwinged Plovers were found in sites ranging from pan edges (muddy substratum and adjacent grass lawns), cultivated lands, burnt grasslands, clearings in thickets and open to closed woodlands. When habitat use is measured as the number of birds per habitat multiplied by the number of days that the birds were seen there (= bird-days), then the following pattern of habitat use is seen: mudflats - 876 bird-days; cleared lands - 1263 bird-days; burnt grassland - 1288 bird-days; ; woodlands - 8689 bird-days. In all sites with grass, grass height was less than 5 cm (pers. obs.). Although Lesser Blackwinged Plovers fed in a wide variety of habitats they always returned to roost in woodlands at night. Lesser Blackwinged Plovers did not feed in open grasslands with short grass but moved into burnt grasslands shortly after a burn to feed opportunistically on scorched invertebrates (pers. obs.). Members of this species nested in a 5000 m^2 clearing in a thicket (all five nests within 2 m of the edge of the thicket) and in woodlands. The woodlands varied considerably in structural composition (Table 1.1). The dissimilarity matrix derived from M.C.D. values (Cain & Harrison 1958) (Table 1.2) and the resultant Bray & Curtis (1957) ordination revealed (Fig. 1.3) some similarity between the woodlands with a few woodlands quite different from the others. Only four Lesser Blackwinged Plover nests (13% of the total found during the study period) were found in the outlier woodlands H-J. All the nests found in these woodlands were constructed at least 20 days after the construction of the last nest of each year in the group of woodlands A-G. It appears that these unusual woodlands are occupied perhaps as a result of intraspecific competition for nest-sites or territories by submissive or juvenile birds. If these woodlands are removed from the analysis then the woodlands chosen for nest-sites by Lesser Blackwinged Plovers are relatively uniform (<u>e.g.</u> mean ±S.E. canopy cover of all woodlands is 39,1 ±7,4% compared with 25,72 ±2,64% for woodlands A-G. The lower standard error indicates the relative uniformity of woodlands A-G). There was a fairly strong negative correlation

Table 1.1. The structural composition of woodlands occupied by Lesser Blackwinged Plovers.

Woodland	Tree density (trees/100m^2)	Canopy area (m^2)	Canopy cover (%)	Ht. of trees (m)	Ht. to lowest pt. of canopy (m)	Canopy depth (m)
A^1	1,42	10,37	14,73	3,11	0,73	2,38
B^1	2,09	9,52	19,90	2,43	0,38	2,05
C^1	1,35	21,40	28,89	5,63	3,11	2,52
D^1	2,05	17,83	36,55	5,18	1,95	3,23
E^1	1,24	20,60	25,54	8,33	4,00	4,33
F^{1,2}	1,19	21,22	25,25	8,16	4,31	3,85
G^1	2,30	20,00	46,00	4,86	1,60	3,26
H^1	0,54	164,48	88,82	9,16	3,98	5,18
I^1	0,72	40,52	29,17	4,94	1,30	3,64
J^1	1,36	45,95	62,49	11,00	3,70	7,30
K^2	0,11					

= used by Lesser Blackwinged Plover

= used by Crowned Plover

= *Acacia nilotica* woodland

= *A.nilotica*

= *A.tortilis*

= *A.tortilis*/*A.nilotica*

= *A.nigrescens*

= *A.nilotica*

= *Sclerocarya caffra*

= *A.nilotica*

= *A.nigrescens*

= *A.tortilis*/*A.nilotica*/*S.caffra*

Table 1.2. Dissimilarity matrix based on the structural composition of woodlands occupied by Lesser Blackwinged Plovers, using M.C.D. values (see text - p. 20) (Cain & Harrison 1958).

	A	B	C	D	E	F	G	H	I
A									
B	1,44								
C	3,52	3,22							
D	5,32	4,44	2,15						
E	4,29	3,66	1,76	3,62					
F	4,17	3,54	1,76	3,62	0,26				
G	3,76	3,13	0,92	2,00	2,19	3,03			
H	17,41	16,79	13,55	12,35	13,14	14,71	13,65		
I	7,13	6,23	4,23	2,08	5,69	6,55	3,83	10,64	
J	12,72	12,09	8,88	7,65	8,60	8,34	9,22	6,28	5,94

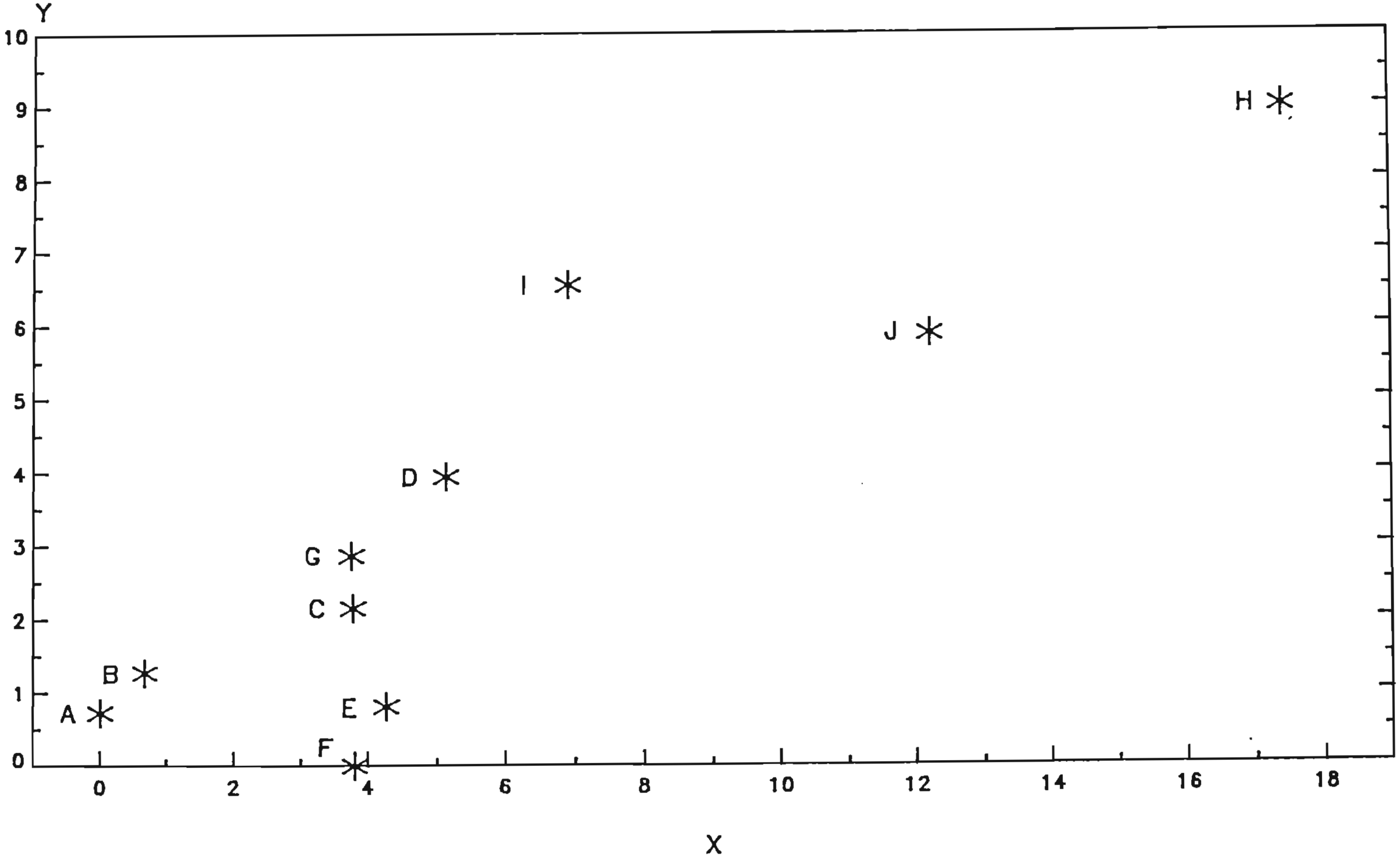


Fig. 1.3. Bray-Curtis ordination of woodlands near Ndumu occupied by Lesser Blackwinged Plovers. The correlation of this ordination with the dissimilarity matrix using M.C.D. values (see text page 20) was highly significant ($\underline{r}$ = 0,996; $p < 0,001$).

between tree density and canopy cover ($\underline{r}$ = -0,716; $p < 0.05$).

DISCUSSION

Distribution

Crowned Plovers are widespread in Natal, but are not present at altitudes above 1500 m a.s.l. While altitude itself is not likely to be the factor limiting the distribution of Crowned Plovers, it is strongly correlated with other variables such as temperature. Since Crowned Plovers even occur in very arid grasslands in Namibia (Winterbottom 1971) and in moist highland grasslands (pers. obs.), it is unlikely that rainfall restricts their distribution. However, because Crowned Plovers prefer short grass areas, low rainfall or a well defined dry season is advantageous to them (as it is to Blackwinged and Lesser Blackwinged Plovers) because it limits grass growth. Low rainfall provides acceptable conditions for this species as long as it does not have a detrimental effect on food availability. It is likely that the major factor limiting the distribution of the Crowned Plover in Natal is temperature, more specifically low minimum temperatures experienced in areas above 1500 m a.s.l., and >15 ^{O}C effective temperature.

Blackwinged Plovers preferred altitudes of between 900 m and 1500 m a.s.l., although they were also found up to 1800 m and down to

300 m a.s.l. (Cyrus & Robson 1980). Blackwinged Plovers have also been recorded at sea level in Natal (Cyrus 1982, pers. obs.), which appears to call the usefulness of the measure of preference used (Fig. 1.2) into doubt. However, since the Blackwinged Plover only rarely occurs below 300 m a.s.l. in Natal, this measure is still a useful indicator of relative preference within the species. Blackwinged Plovers have usually been recorded from the coastal areas in the cooler, winter months of May-July (pers. obs.) although Cyrus (1982) has recorded this species breeding on the Hluhluwe River floodplain near sea level in September. Altitude does not influence Blackwinged Plover distribution because they are found at sea level all year in the eastern Cape. It would appear then that Blackwinged Plovers have a distinct preference for the 15-16 ^{o}C effective temperatures in Natal and are found within these isolines (Stuckenberg 1969) as these lines traverse the coast in the eastern Cape.

Lesser Blackwinged Plovers are found only below 300 m a.s.l. in Natal and occur in southern Africa in the lowland areas of the eastern Transvaal, Swaziland and northern Natal. Altitude is not the major factor affecting the distribution of Lesser Blackwinged Plovers because it is not found further down the coastal plain than Lake St. Lucia. This distribution is above Stuckenberg's (1969) >18^{o}C effective temperature.

The parapatric distributions of two closely related species, such as is the case with Blackwinged and Lesser Blackwinged Plovers, has been attributed to competitive exclusion between the two species (Diamond 1975). However, because of the lack of observed interspecific competition when these two species concur, this hypothesis must be rejected in this case. It is more likely that the parapatric distributions of these two species are a result of adaptations to different climatic conditions which happen to cause parapatry.

Niche selection

Blackwinged Plovers are niche specialists, occurring only in short or burnt grasslands with very few or no trees. Crowned Plovers are also relatively specialized in their niche occupation, occurring only in short or burnt grasslands, opportunistically in cultivated fields and rarely in very open woodlands. Lesser Blackwinged Plovers are, relative to Crowned and Blackwinged Plovers, niche generalists since they are found in muddy areas near pans, grass lawns near water, cultivated fields, burnt grasslands, clearings in thickets and open woodlands. All three species, which are cursorial insectivores which feed by picking items off the substratum, occupy habitats characterized by the shortness of the grass (< 5 cm) or the lack thereof, which facilitates both mobility and visibility.

Role of competition in habitat selection

Differential habitat use by members of a species or by ecologically similar sympatric species has often been recorded and ascribed to either inter- or intra-specific competition (e.g. Selander 1966; Diamond 1975). However, there is no evidence to support the existence of interspecific competition between these species. Crowned and Blackwinged Plovers feed together in mixed-species flocks and, on occasion, occupy adjacent nesting territories. The association between Crowned and Lesser Blackwinged Plovers and between Blackwinged and Lesser Blackwinged Plovers is relatively rare because of minimal overlap of habitat use, although when they do concur no interspecific aggression has been noted. Crowned and Lesser Blackwinged Plovers have been seen feeding and roosting in mixed-species flocks in burnt grasslands and cultivated lands (Diamond pers. comm.; pers. obs. (n = 16 occasions)), while Blackwinged and Lesser Blackwinged Plovers have been seen feeding in mixed flocks (pers. obs. (n = 5 occasions)).

Intraspecific competition for nesting and, occasionally, feeding territories occurs in all three species (see Chapters 3 and 5). Since all three species usually nest in loose colonies (pers. obs.), those individuals that nest alone may do so as a result of intraspecific competition. Thus, the unusual use by Crowned Plovers of open woodlands to nest in may be a result of intraspecific competition for nest sites in the nearby (5 km away) Ndumu Estates grassland where intraspecific aggression is common (see Chapter 4) between the 15-20 pairs nesting there in a 16-ha area. In the case of Lesser Blackwinged Plovers, a single pair nested in woodlands H and J respectively, despite the structure of these woodlands being quite different to the others occupied by this species (Fig. 1.3), suggesting that intraspecific aggression may have caused the use of these woodlands. There was no evidence of any Blackwinged Plovers altering their habitat selection because of intraspecific aggression.

Role of predation in habitat selection

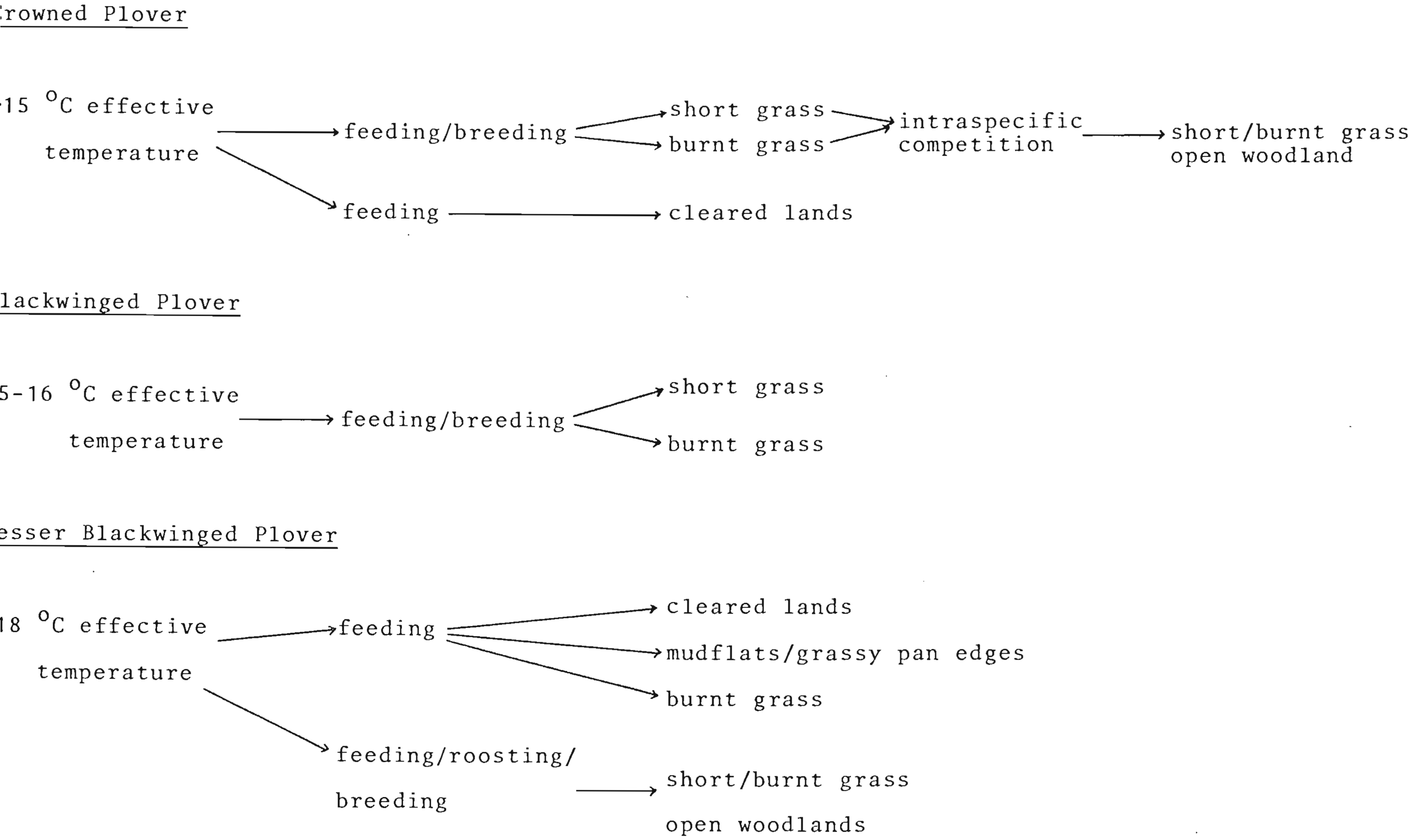
Crowned and Blackwinged Plovers live in open grasslands and so do not appear to take steps to enhance crypsis to avoid predation. Lesser Blackwinged Plovers always nest in woodlands and roost there at night even if they are feeding in open areas. Woodlands used by Lesser Blackwinged Plover show a fairly strong negative correlation between tree density and canopy cover, i.e. as tree density increases canopy cover decreases. This correlation suggests that these birds are selecting for a certain overall visibility in order to detect predators easily and at the same time to reduce their detectability by predators. The reason that Lesser Blackwinged Plovers occur in open rather than closed woodlands (where they may be less visible to predators) may be that, once stem density increases to a certain point, then area of ground for searching for prey decreases to an unacceptable level.

CONCLUSIONS

Crowned and Blackwinged Plovers overlap considerably in habitat selection within the range of Blackwinged Plovers. Blackwinged and Lesser Blackwinged Plovers are largely allopatric while Crowned and Lesser Blackwinged Plovers overlap in distribution but rarely in niche selection. For this reason, a study of the feeding ecology of Crowned and Blackwinged Plovers would be of particular interest.

The distribution of all three species appears to be controlled, at least to a certain extent, by effective temperature. Stuckenberg's (1969) model, previously applied only to ectothermic animals, may be a useful way of analyzing the distributions of these and other avian species.

The primary habitat requirement of Crowned, Blackwinged and Lesser Blackwinged Plovers is that the ground vegetation be short. Other important factors are the lack of trees (Blackwinged Plovers), not too many trees (Crowned Plovers) and open woodlands to roost and nest in (Lesser Blackwinged Plovers). Fig. 1.4 shows a hypothetical series of factors influencing habitat selection in Crowned, Blackwinged and Lesser Blackwinged Plovers.



g. 1.4 Hypothetical factors influencing habitat selection by Crowned, Blackwinged and Lesser Blackwinged Plovers.

Chapter 2

COEXISTENCE OF CROWNED AND BLACKWINGED PLOVERS

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Summary. Coexisting crowned plovers _Vanellus coronatus_ and blackwinged plovers _V. melanopterus_ were studied to determine whether niche partitioning occurred or was necessary to facilitate their coexistence. The results of this study show that niche partitioning did not occur. We suggest that the association of these two species potentially enhances the ability of each to detect and avoid predation, in spite of any possible deleterious effect of interspecific competition (_e.g._ reduced _per capita_ food intake).

INTRODUCTION

Crowned plovers *Vanellus coronatus* and blackwinged plovers *V. melanopterus* inhabit areas of short or burnt grassland in eastern and southern Africa. Where these two species occur sympatrically in southern Africa, they are often found feeding and roosting together (Skead 1955, Maclean 1985). This association was studied from January 1985 to December 1986 with particular reference to interspecific aggression, cooperation, time and rate of feeding, and vigilance.

The two species are similar in mass (crowned plover = 160-200 g, blackwinged plover = 160-175 g) and might be expected to have similar feeding requirements. They also overlap in range of culmen length (crowned plover = 28-33 mm [$\bar{x}$ = 30.3 mm], blackwinged plover = 25-29 mm [$\bar{x}$ = 26.8 mm]). Differences in culmen length have been considered to account for resource partitioning in sympatric bird species (e.g. Hutchinson 1959, Schoener 1965). Hutchinson (1959) suggested that a culmen-length ratio (of the larger species' culmen to that of the smaller) of 1:1.3 could be used as an indication of the difference in culmen length necessary to permit two species to concur in different niches at the same level of a food web. The ratio of the mean culmen length of crowned to blackwinged plovers is 1:1.13. The aim of this study was, in the light of the morphological similarity of these two species, to determine whether spatial or temporal partitioning of food resources occurs and whether this is necessary for these two species to coexist.

METHODS

Associations of crowned and blackwinged plovers were studied near Pietermaritzburg, South Africa, mainly at the Scottsville Racecourse (an area of open grassland of about 20 ha) and at four similar areas nearby (Fig. 1). The Scottsville Racecourse differed from the other four study sites and from most other sites occupied by these birds in that it was mown weekly and so remained suitable for vanelline plovers throughout the year.

Grass-height preferences were examined at Ukulinga Research farm only, in 24 plots (each 25 m x 25 m in area) with different cattle-grazing regimes and, therefore, different grass heights. Grass height was measured by the point-intercept method (Mueller-Dombois & Ellenberg 1974) once a week for the 8-week trial period. Grass cover in each plot was 100%.

Because vanelline plovers are extremely wary, only 22 crowned plovers and one blackwinged plover were captured in 1985 and a further 21 crowned plovers and 14 blackwinged plovers in 1986. These plovers were caught in mist nets and by spotlight techniques (Graul 1979) and colour-banded for individual recognition.

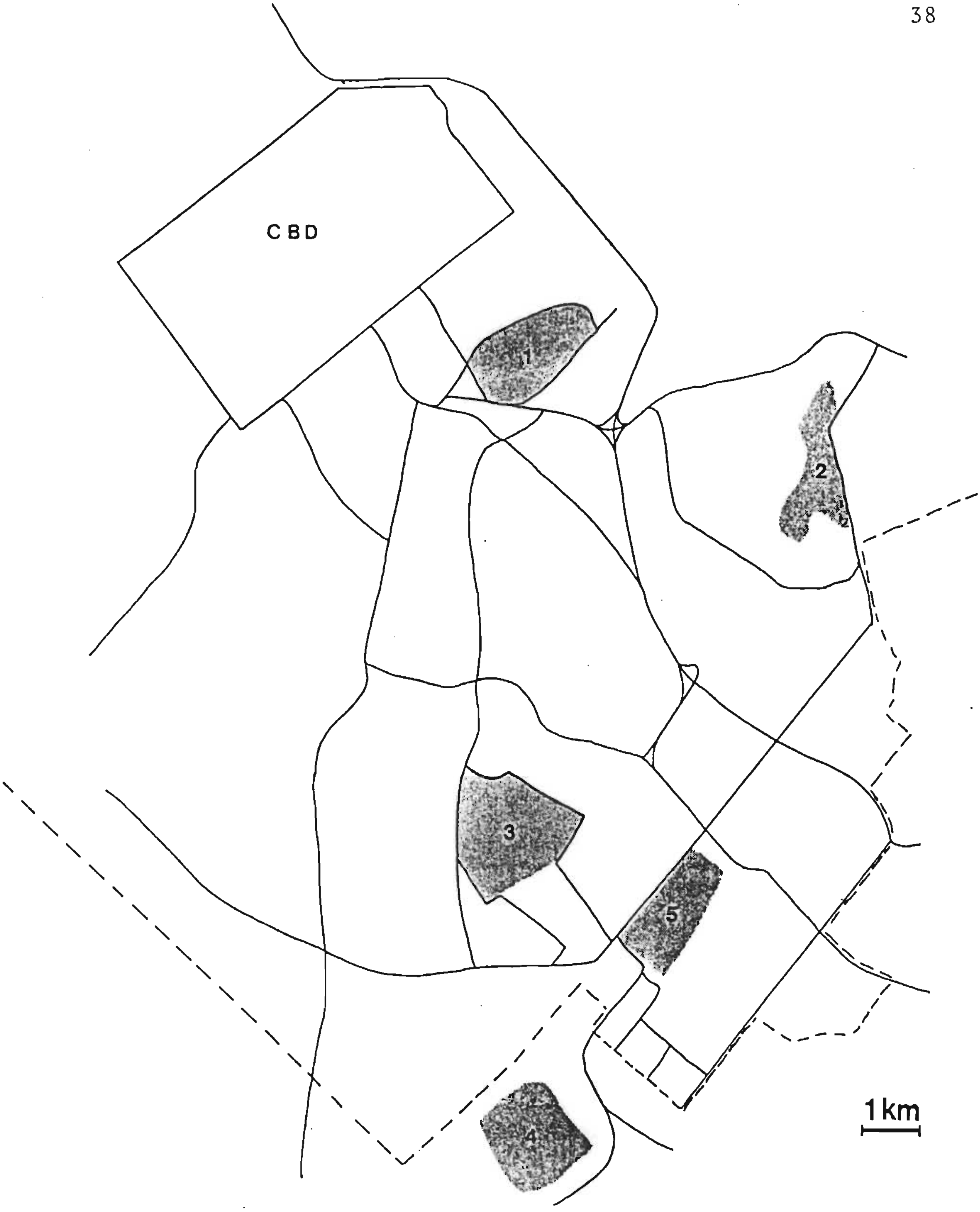

Fig. 1. Schematic diagram of Pietermaritzburg showing major study sites. 1 = Scottsville Racecourse; 2 = Roy Hesketh Park; 3 = Oribi Airfield; 4 = Ukulinga Research Farm; 5 = Scottish Cables grassland; CBD = Central business district of Pietermaritzburg.

Census counts of the crowned and blackwinged plovers at Scottsville Racecourse were made twice a day (during feeding periods in the morning and afternoon) 10 times a month. Associations of plovers were also recorded.

Feeding rates of the two species were determined in 1985 by counting the number of pecks per minute by a focal bird for five minutes at a time, yielding five separate counts of pecks per minute. The feeding rate was determined only when birds of both species were within 20 m of one another and thus likely to be faced with the same food resources. Feeding rates were determined in alternate 5-min periods for the two species by the number of pecks per minute because prey was usually so small that swallowing could not be detected.

Vigilance of both crowned and blackwinged plovers was measured in flocks of different sizes by the number of scans for predators per bird per minute. Scans were treated as though they were of equal duration since they were so short that observer-reaction time, when using a stopwatch, would introduce an unacceptable amount of experimental error. Mean nearest-neighbour distances (Goss-Custard 1980) were compared for different flock sizes in order to determine changes in behavior relative to flock size. This was measured by comparison with objects set at known distances in the feeding areas. For night observations, we used a light-intensifying telescope.

In 1986, in an attempt to improve the accuracy of feeding-rate and vigilance measurements, instantaneous behavior sampling (Altmann 1974) was used. Every 15 s the behavior of a bird was recorded as either pecking, walking, scanning, flying, intraspecific aggression, inter-specific aggression, resting or preening to determine frequency of occurrence of each activity.

In order to measure the size range of arthropods available to the plovers, a 0.25-m^2 x 10-cm high quadrat was thrown to the ground every 5 m along a straight line through a plover feeding area and the arthropods counted therein. One hundred points were sampled at a time, 10 times a month in 1986. Sampling was done only while the plovers were feeding. The quadrat was covered with burlap to prevent flying and saltatory arthropods from escaping. This quadrat was used because it was the only effective method of counting termites in the grassland.

Sonagrams of alarm calls were produced using a Voice identification III Series 700 audio spectrograph using a wide-band filter (300 Hz) from a Gillard (1983) recording.

The reactions of blacksmith plovers _Vanellus armatus_, African wattled plovers _V. senegallus_ and lesser blackwinged plovers _V. lugubris_ to crowned and blackwinged plover alarm calls were observed in northern Natal.

RESULTS

Habitat preferences

Crowned and blackwinged plovers occupied the same (7) plots simultaneously at Ukulinga over the entire trial period. Mean ±S.E. grass height in preferred plots was 4.23 ±0.16 cm. Mean maximum grass height was 5.70 cm while the mean minimum was 2.32 cm. The shortest grass height in plots not used by plovers was 6.24 ±0.35 cm.

Behavior

There was a strong positive association between Crowned and Blackwinged Plovers on the Scottsville Racecourse in all months when Blackwinged Plovers were present there (Table 1).

The Scottsville Racecourse infield area had two main roost sites in summer and autumn (November-April) of 1985 and 1986 (Figs 2a and b), both on ground elevated above the surrounding feeding area. Based on observations of the marked birds, these two flocks appeared not to associate with each other, each feeding in the vicinity of its roosting area. From the onset of winter (May) until the end of October each year only roost site A (Figs 2a and b) was used by all the plovers on the racecourse. Roosts were occupied during periods of low and high temperatures (below

Table 1. Degree of association of crowned and blackwinged plovers at Scottsville Racecourse in 1985 and 1986, using Cole's (1949) index of interspecific association. 100% positive association = 1; 100% negative association = -1. * = no blackwinged plovers on racecourse, at breeding sites elsewhere.

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC
1985											
1	1	1	0.96	0.84	0.90	1	*	*	*	1	0.94
1986											
1	0.81	0.91	0.85	0.84	0.94	1	*	*	*	0.83	0.83

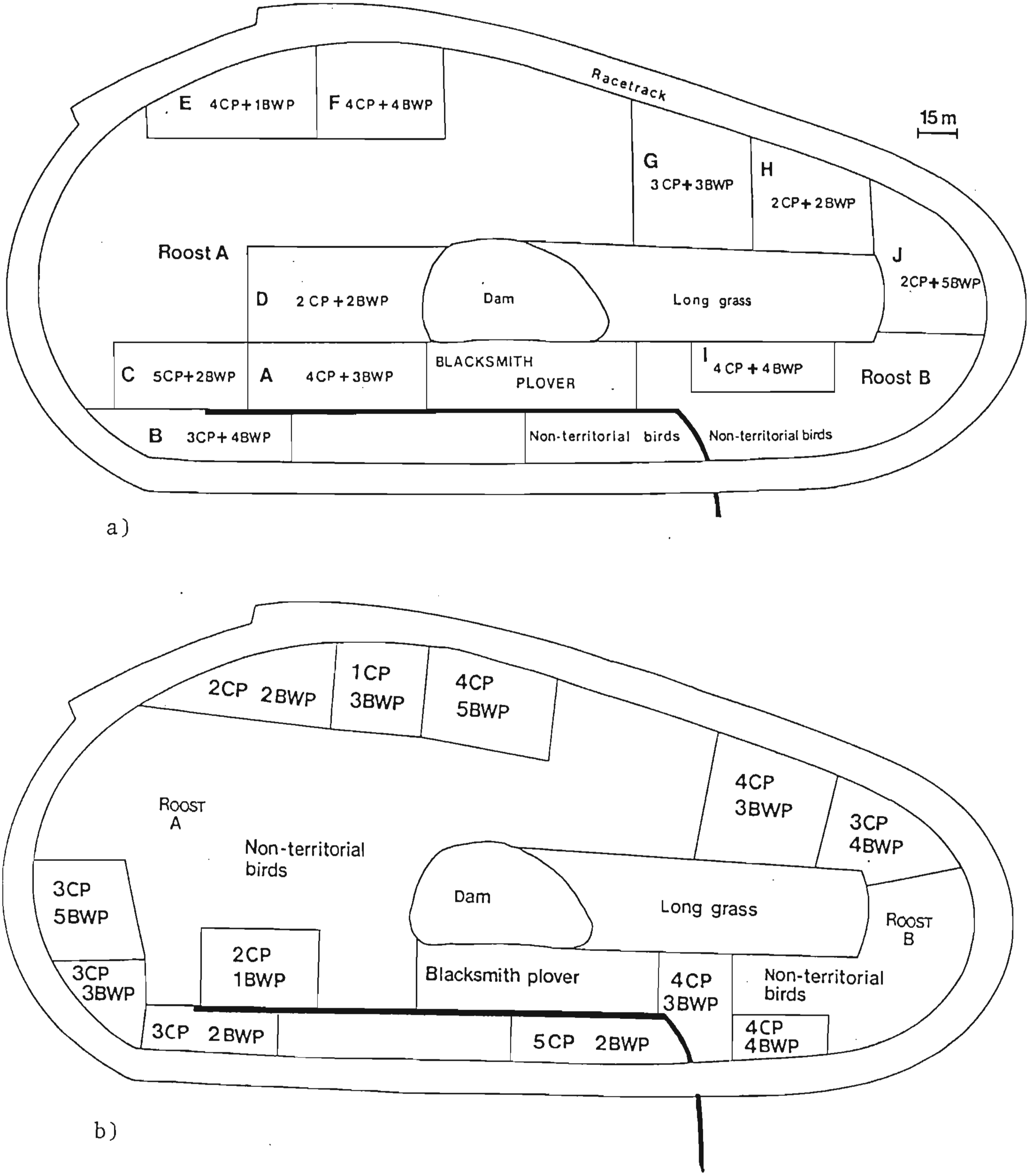

Fig. 2. Schematic representation of crowned and blackwinged plover territories on Scottsville Racecourse in 1985 (a) and in 1986 (b). BWP = Blackwinged plover; CP = Crowned plover. Scale: 1 cm = 15 m.

10^{o}C and above 24^{o}C) when the birds did not feed, and at night.

On the Scottsville Racecourse and on the four other study areas, both crowned and blackwinged plovers separated into territorial and non-territorial groups during the nonbreeding period (October -July) but all birds used the same roost site. Territorial groups consisted of 2-5 birds in each species. Territories ranged in size from 0.56-0.83 ha. It is not known whether the members of a territorial group are related, although territorial groups contained both birds in juvenile plumage and one pair of adults at least until the end of March each year. After the end of March, we were unable to distinguish young birds from adults. Two crowned plover pairs and their broods of two and three young were colour-banded in September 1985 and remained together as territorial groups until the onset of the following breeding season (August 1986). Any one territory might be occupied by a group of both species (Figs 2a and b). The territories occupied in 1986 were not all the same as those occupied in 1985, nor were the same combinations of birds of each species present when the same territorial area was occupied (Figs 2a and b). Territories were not occupied for the entire summer in 1986, although they were in 1985. Non-territorial groups consisted of up to 30 birds and fed in areas ranging from 1.4-2.6 ha. Six marked birds (five crowned plovers and one blackwinged plover) were non-territorial and remained on the racecourse for periods varying from 4 h to several days at a time.

A territory was defended by both crowned and blackwinged plovers only against conspecifics. Both species evicted intruders by means of aggressive vocalizations, aggressive threat displays (Skead 1955; Maclean 1972) and aerial mobbing. However, aggression was usually employed only during the establishment of territories. When these territories were being established, members of either species fought with conspecifics and ignored members of the other species present in the territory. Territories were usually maintained by what appeared to be mutual avoidance. The few cases of territorial aggression observed after territories had been established (crowned plovers n = 5; blackwinged plovers n = 2) appeared to occur only when a group of plovers new to the area (as indicated by a sudden increase in the total number of plovers present) intruded on an established territory.

In grassland areas which were not mown crowned and blackwinged plovers did not form territories, but rather remained in flocks of up to 70 birds of each species. These flocks moved whenever the grass got taller than about 5 cm, or when food availability dropped below an acceptable level (as indicated by a feeding rate of lower than about 0.5 pecks/minute). Mixed-species flocks were usual and all the birds in a mixed-species flock fed and roosted together.

With the onset of winter, most of the plovers (both on and off the racecourse) split up into smaller groups of 2-3 birds.

However, when a group of one species was joined in an area of grassland by a group of the other species, the birds usually fed as a single group. On the Scottsville Racecourse, roost site A was used throughout each winter by members of both species during non-feeding periods in 1985 and 1986, even if they were not feeding on the racecourse. The number of plovers using this roost site in winter varied from 10 to 60 birds.

Interspecific aggression

Our study confirms the observations of Skead (1955) that there were few interspecific aggressive interactions between crowned and blackwinged plovers when feeding together. In 1000 observation hours, blackwinged plovers chased crowned plovers away from a food item on six occasions, while crowned plovers twice chased blackwinged plovers away from food.

Cooperation

Upon entering a feeding territory, territorial crowned and blackwinged plovers initially fed in a random pattern. After 15-30 min, all the birds in a feeding territory arranged themselves abreast virtually in a straight line and moved up and down the feeding area, spaced at regular intervals from one another. When feeding like this, crowned and blackwinged plovers were not necessarily separated into two species groups but were often irregularly distributed along the line.

The initial response of blackwinged plovers to aerial and terrestrial predators was to remain silent and still. Crowned plovers, on the other hand, uttered noisy alarm calls and bobbed their bodies in a defensive threat display (Maclean 1972). If the predator approached still further, both territorial and non-territorial birds of both species uttered alarm calls, which drew all the vanelline plovers together (including any blacksmith and African wattled plovers that were present). They then collectively mobbed the predator until it departed. Even birds which were up to 750 m away, and not visible to the predator, would rush to the scene of alarm. Lesser blackwinged plovers did not respond to crowned and blackwinged plover alarm calls.

There was no significant change ($p > 0.05$) in scanning rate (= vigilance) for either species with increasing flock size up to the largest flock size for which this was measured (eight birds). However, the two adult birds of family groups of each species in mixed-species flocks took turns to stay vigilant, irrespective of the vigilance behavior of either the immature birds of their respective species or the members of the other species ($n = 10$ pairs of each species, over a total of 500 min of observation for each species using instantaneous behavior sampling). The mean ±S.E. number of scans per minute by crowned plovers (regardless of flock size) was 6.72 ±0.32 ($n = 500$ min), while the mean ±S.E. number of scans per minute for blackwinged plovers was 6.39 ±0.43 ($n = 500$ min). The difference in scanning rate of the two species was not significant (t_{998} = 0.62). Nearest-neighbour distance in mixed-species flocks increased from a flock size of two up to five (Fig. 3) where it reached an asymptote. At night (n = 55 hours of observation) and when it was misty (n = 17 hours of observation), birds of both species remained within 1 m of each other, regardless of flock size.

Feeding ecology

Crowned and blackwinged plovers spent similar amounts of time feeding in summer. All members of both species in each feeding area started and stopped feeding simultaneously. Members of both species stopped feeding when the temperature reached about 24^{o}C, which is usually shortly after 09h00 in Pietermaritzburg in summer, and resumed feeding when it dropped below this temperature, at about 16h00. Neither species fed when the temperature dropped below 10^{o}C.

The fact that blackwinged plovers fed at a faster rate than crowned plovers (Fig. 4) in summer 1985 supports field observations that blackwinged plovers were more opportunistic than crowned plovers, since blackwinged plovers moved about quickly, picking up items with little hesitation, while crowned plovers moved more slowly, stopped moving and then lunged at a prey item.

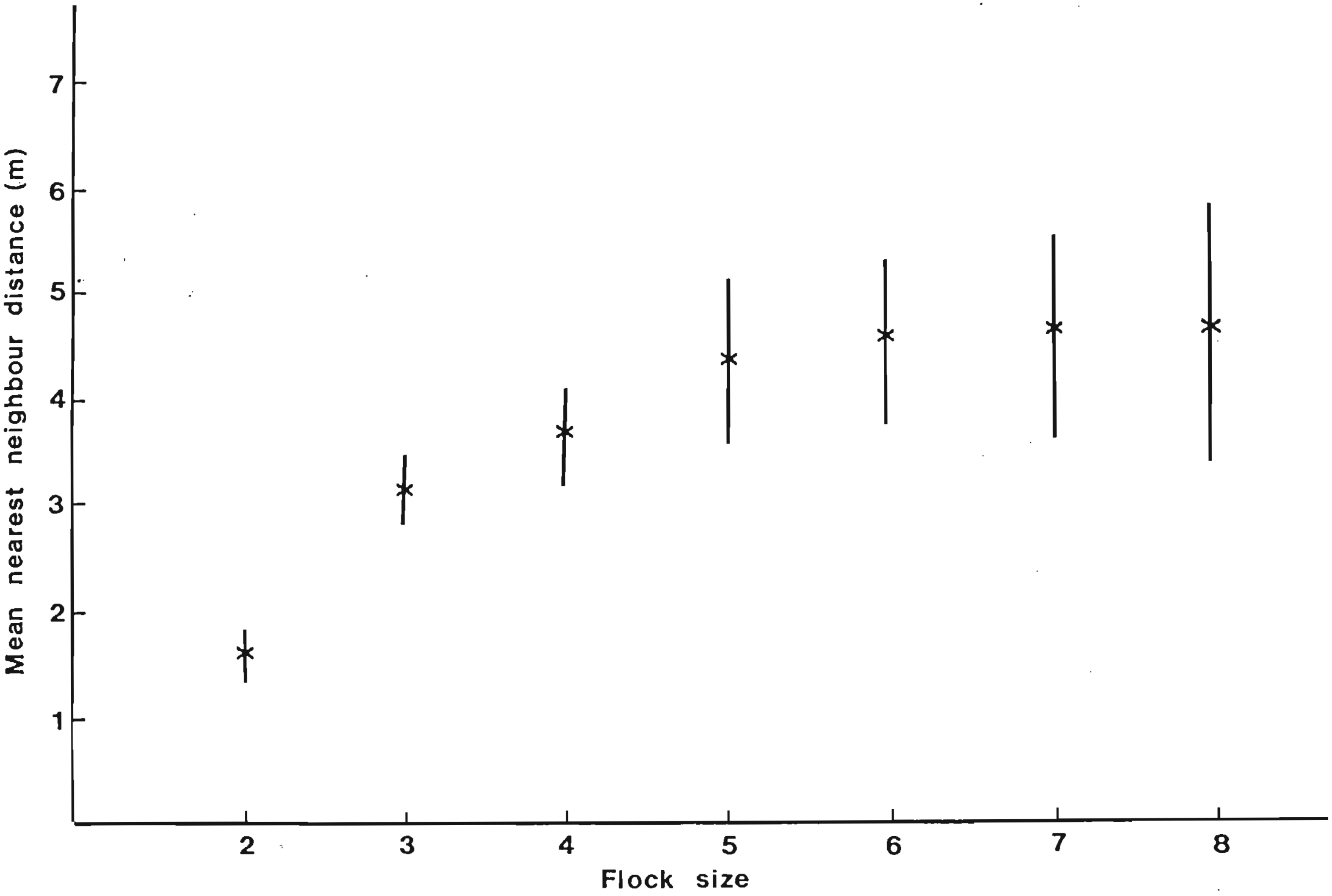

Fig. 3. Mean nearest-neighbour distance relative to flock size for mixed flocks of crowned and blackwinged plovers (n = 500 min for each mean value). Means and 95% confidence limits are plotted.

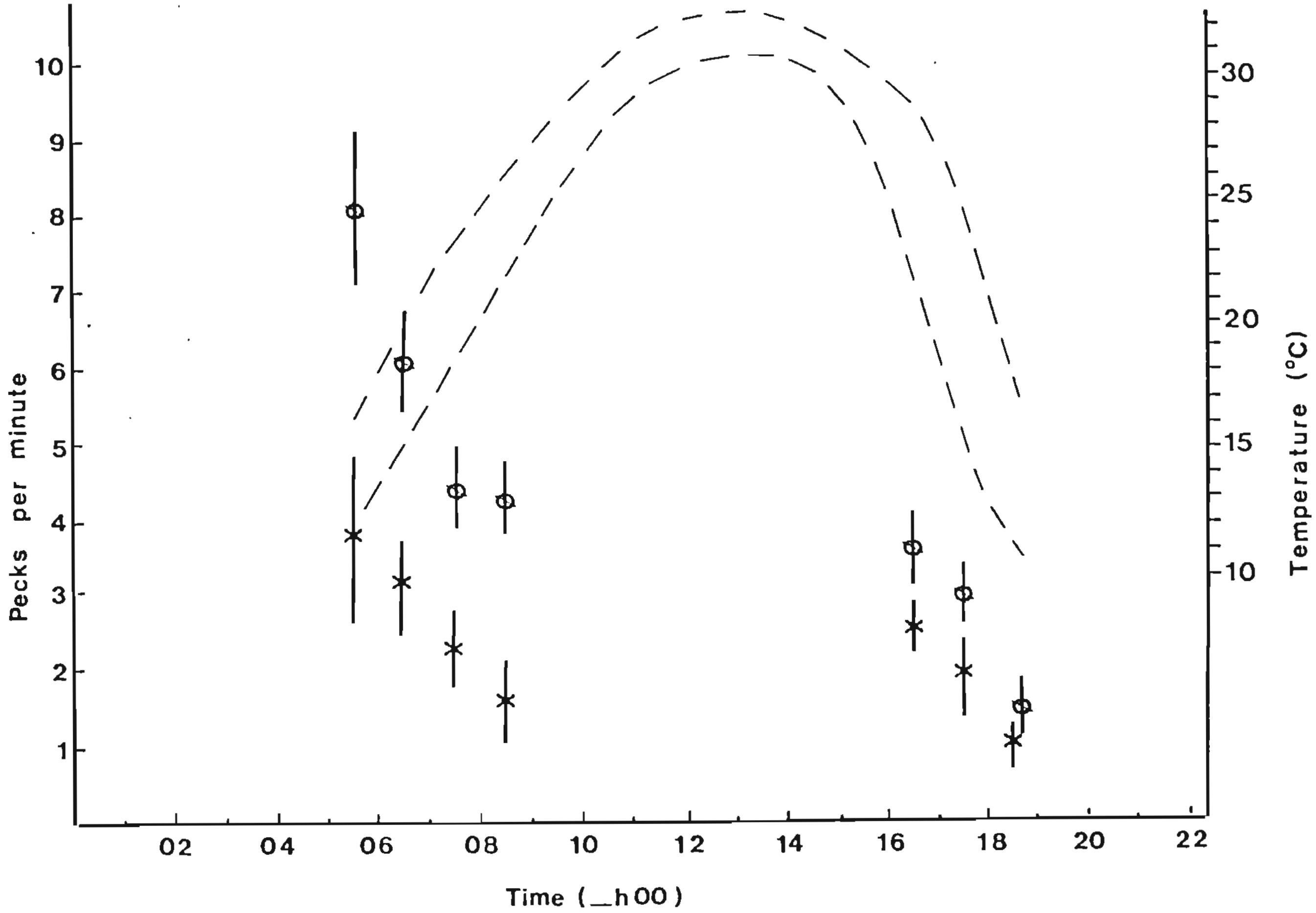

Fig. 4. Feeding rates of crowned and blackwinged plovers in summer 1985 measured as pecks per minute. Temperature range lies between the dotted lines. Means and 95% confidence limits for feeding rates of crowned (x) and blackwinged (ɸ) plovers are plotted (n = 500 min for each mean value).

In winter, crowned and blackwinged plovers fed for varying periods throughout the day. Feeding rates were measured only when members of both species were feeding together and then pooled for each species for the entire winter of 1985. Mean ±S.E. number of pecks per minute for crowned plovers during this period was 1.12 ±0.02 (n = 500 min), while the mean ±S.E. number of pecks per minute for blackwinged plovers was 1.06 ±0.04 (n = 500 min). There was no significant difference in the two species' feeding rates (t_{998} = 0.01).

Instantaneous sampling of plover behavior showed that crowned plovers lowered their vigilance significantly when in the presence of blackwinged plovers and spent more time feeding and searching for food (Table 2). Blackwinged plovers, on the other hand, spent significantly more time vigilant and less time feeding in mixed-species flocks with crowned plovers.

Examination of 200 fecal samples of each species taken in winter (May - August) 1985 indicated that, measured as the number of mandibles present (since this was the only arthropod body-part that was consistently preserved in the feces), the diet of the two species was very similar (Table 3), assuming that the ability of the two closely-related plover species to digest different prey species is similar. The gizzard contents of five crowned plovers and five blackwinged plovers shot while feeding together at Scottsville Racecourse in May 1987 were similar (Table 4). The

Table 2. Instantaneous behavior sampling during active foraging bouts measured as proportions of total time spent during foraging. Pecking and walking were pooled as feeding activity in G-tests for differences in behavior of single- and mixed-species flocks.

BWP = blackwinged plover; CP = crowned plover.

a) Crowned plover (n = 2560 x 15 s intervals)

Behavior category	With BWP	Without BWP	
Feeding	0.51	0.39	p <0.001, G-test
Scanning	0.49	0.61	

b) Blackwinged plover (n = 2560 x 15 s intervals)

Behavior category	With CP	Without CP	
Feeding	0.43	0.50	p <0.01, G-test
Scanning	0.57	0.50	

Table 3. Analysis of feces of crowned and blackwinged plovers in winter 1985 (n = 200 fecal samples of each species). CP = crowned plover; BWP = blackwinged plover.

Prey	CP	BWP
Odontotermes sp.	79.3%	83.7%
Tenebrionidae	8.5%	1.5%
Formicidae (*Dorylus* sp.)	13.2%	10.4%
Araneae	3.9%	2.2%
Orthoptera	0%	2.2%

Table 4. Analysis of gizzards of crowned and blackwinged plovers in May 1987 (n = 5 gizzards of each species).

	Crowned plovers	Blackwinged plovers
Odontotermes sp.	76.4%	90.3%
Tenebrionidae	11.9%	3.2%
Formicidae (Dorylus sp.)	8.0%	4.9%
Araneae	1.4%	0.8%
Orthoptera	2.3%	0.8%

importance of *Odontotermes* sp. in the diet was supported by field observations of both plover species frequently feeding on a patchily-concentrated food source and by chasing the plovers off the feeding area and examining the prey species present.

Monthly quadrat sampling of arthropods available to these plovers in 1986 showed that 95.58% were less than 5 mm long, while a further 3.15% were less than 10 mm in length. There was a strong positive correlation between the combined number of crowned and blackwinged plovers and arthropod availability in 1986 ($r = 0.62$, $p < 0.01$). Data from March and April were excluded as atypical because there was a large increase in the number of plovers resulting from unseasonal rain which brought earthworms (which are usually unavailable to the plovers) to the surface. Earthworms could not be counted using a quadrat.

Breeding coexistence

In 1986, but not in 1985, crowned and blackwinged plovers nested in adjacent territories at three study sites (Fig. 5). Only two cases of interspecific aggression were observed in 480 hours. A blackwinged plover once attacked a crowned plover entering its territory and *vice versa*. Blackwinged plovers do not breed at the Scottsville Racecourse (a low-lying area in suburbia) since they breed only in grassland areas on hilltops. The three breeding sites mentioned above are the only blackwinged plover breeding sites within 20 km of Pietermaritzburg and, as a result,

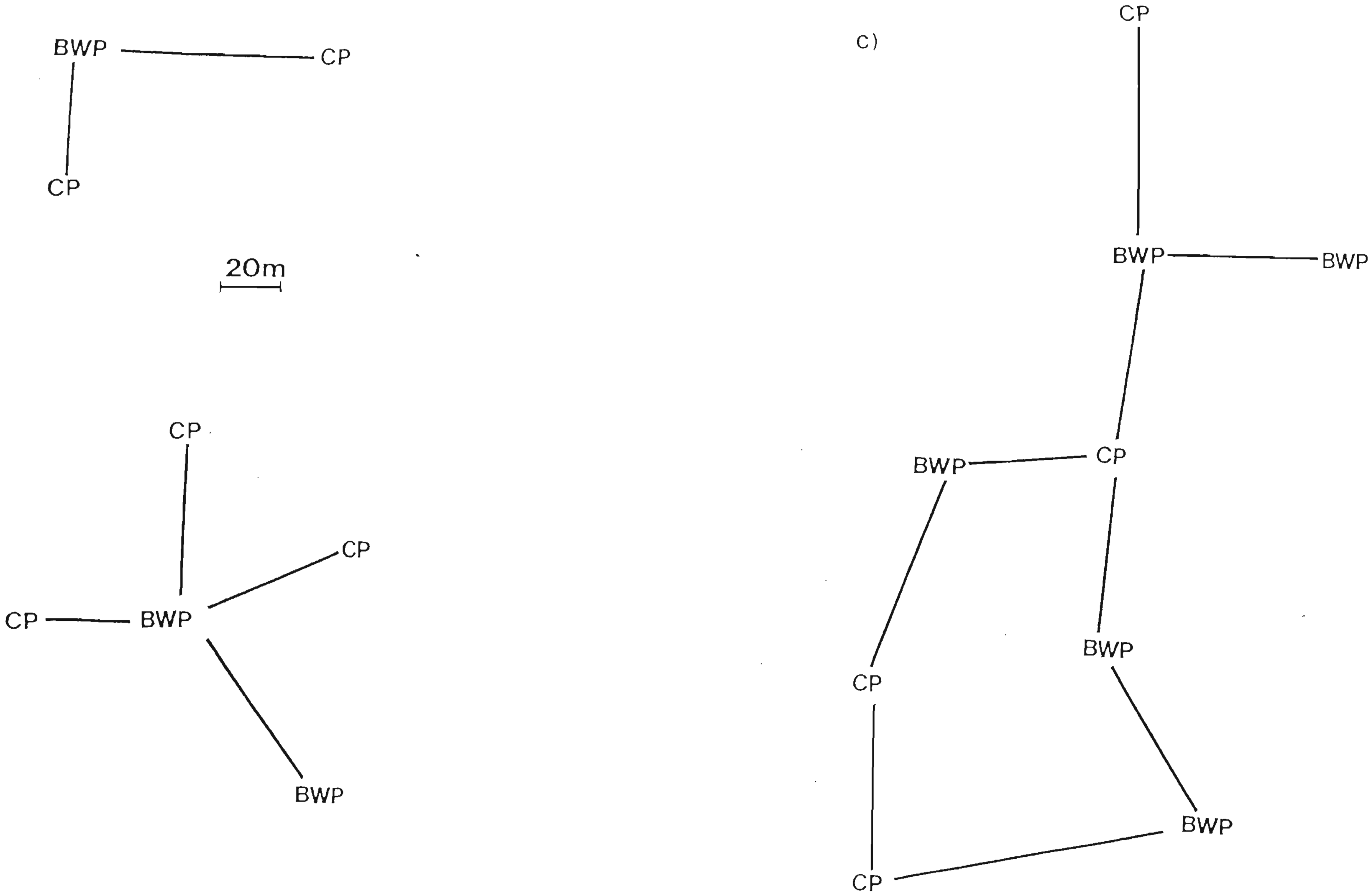

Fig. 5. Schematic representation of nesting territories of crowned and blackwinged plovers in 1986 at Ukulinga Farm, Oribi Airfield and Scottish Cables sites.

most of these birds migrate away from the town in August and return in November. Crowned plovers, on the other hand, do not have a highly specific breeding-habitat preference and breed on any area of short grass.

DISCUSSION

The association of non-breeding crowned and blackwinged plovers in mixed flocks during and their occasional nesting in adjacent territories is in apparent contradiction to interspecific competition theory. The changes in numbers of both species with changing prey availability suggest that diffuse competition (MacArthur 1972) for food occurs. The different feeding rates of these two species in summer indicate, however, that they may have different prey preferences when food is abundant. It is to be expected that any two species may differ in their selection of prey. Blackwinged plovers are habitat specialists since they are restricted in their distribution to temperate areas of South Africa, while crowned plovers are habitat generalists found throughout southern and eastern Africa (Maclean 1985). Cody (1974) suggested that there was a general trend for habitat specialists to be prey generalists while habitat generalists tend to be prey specialists. This might occur because in ecological "crunch" periods habitat specialists may be forced to take whatever prey is available, while habitat generalists can move over a wider area to obtain their preferred prey items.

However, in winter (when food may be scarce) crowned and blackwinged plovers feed on similar prey and still coexist. This indicates that this association occurs in spite of any interspecific competition for food. The small size of prey available to these birds suggests that culmen length is an irrelevant factor in determining feeding separation, since the prey is far smaller than the culmen length of either species. Do these two species derive benefit from this association which counteracts the disadvantages thereof ?

Two major advantages may be gained by flocking behavior:

a) Feeding enhancement: Feeding enhancement for birds feeding in mixed-species flocks has been recorded for a number of species (e.g. Krebs 1973; Kushlan 1978). However, in the case of crowned and blackwinged plovers, if a member of either species finds an area of high prey density, it is immediately joined by all other members of the mixed flock. One species does not compete against another species for control of a patch of high prey density. Rather, these plovers behaved as individuals in catching prey in such a patch, each bird feeding without aggression towards any other bird present. Therefore feeding rate may be enhanced in a flock because each bird may capitalize on patches of high prey density that it might not necessarily have found itself or might have taken longer to find. The plovers' tendency to feed abreast in a straight line may increase their ability to observe each other's feeding rates. However, their lack of interactive behavior with members of the other species means that feeding enhancement is not necessarily greater (for any one species) in a mixed-species flock than in a single-species flock of the same size.

b) Predator avoidance: The advantages of flocking in terms of predator avoidance have been well documented (e.g. Lack 1954; Goss-Custard 1970; Schoener 1971; Morse 1977). The most frequently postulated reason for flocking in the presence of predators is the "many-eyes" hypothesis, which has been supported by the findings of Powell (1974) and Siegfried & Underhill (1975), among others. This hypothesis suggests that, with more eyes to detect predators, each bird in a flock may be able to spend less time on the lookout for predators and more time searching for food. This occurred in crowned plovers but not in blackwinged plovers, the latter species spending more time vigilant in mixed-species flocks than in single-species flocks.

Both species may gain an advantage from the formation of mixed flocks by the observed increase in nearest-neighbour distances with increasing flock size, allowing these birds to forage over a greater area and therefore to increase the likelihood of finding prey. However, in spite of this, blackwinged plovers have a decreased feeding rate in the presence of crowned plovers because of increased vigilance.

Do blackwinged plovers gain any advantage from this association ?

Blackwinged plovers are less aggressive than crowned plovers and do not approach a predator as closely as the latter species. Only in the pre-laying and breeding periods (until the chicks can fly) do blackwinged plovers get closer than about 10 m when a flock is mobbing a predator, while crowned plovers will actually strike a predator with their outstretched legs or a wing tip. This indicates that blackwinged plovers rely on crowned plovers to ward off predators when in mixed flocks.

Stinson (1980) suggested that a major factor in escaping predation by flocking involved confusing the attacker with a group of essentially indistinguishable individuals. Apparently, when predators cannot "fix" on a specific prey item they find it more difficult to pursue prey successfully (Campbell 1975; Curio 1976). This "confusion effect", Stinson suggests, is potentially greater for conspecific than for heterospecific groups. However, the plumage pattern (with the exception of the crown) of crowned and blackwinged plovers is very similar, which, along with the continual lateral and vertical movements of these birds when flying in a flock, makes them ideally suited to employ the "confusion effect" in avoiding predators.

The fact that these two species, as well as the blacksmith plover and the African wattled plover, cooperate in mobbing predators, even if they are not in direct danger themselves, is probably a response to their very similar alarm-call notes (Fig. 6a, b, c and d). This is supported by the fact that the lesser blackwinged

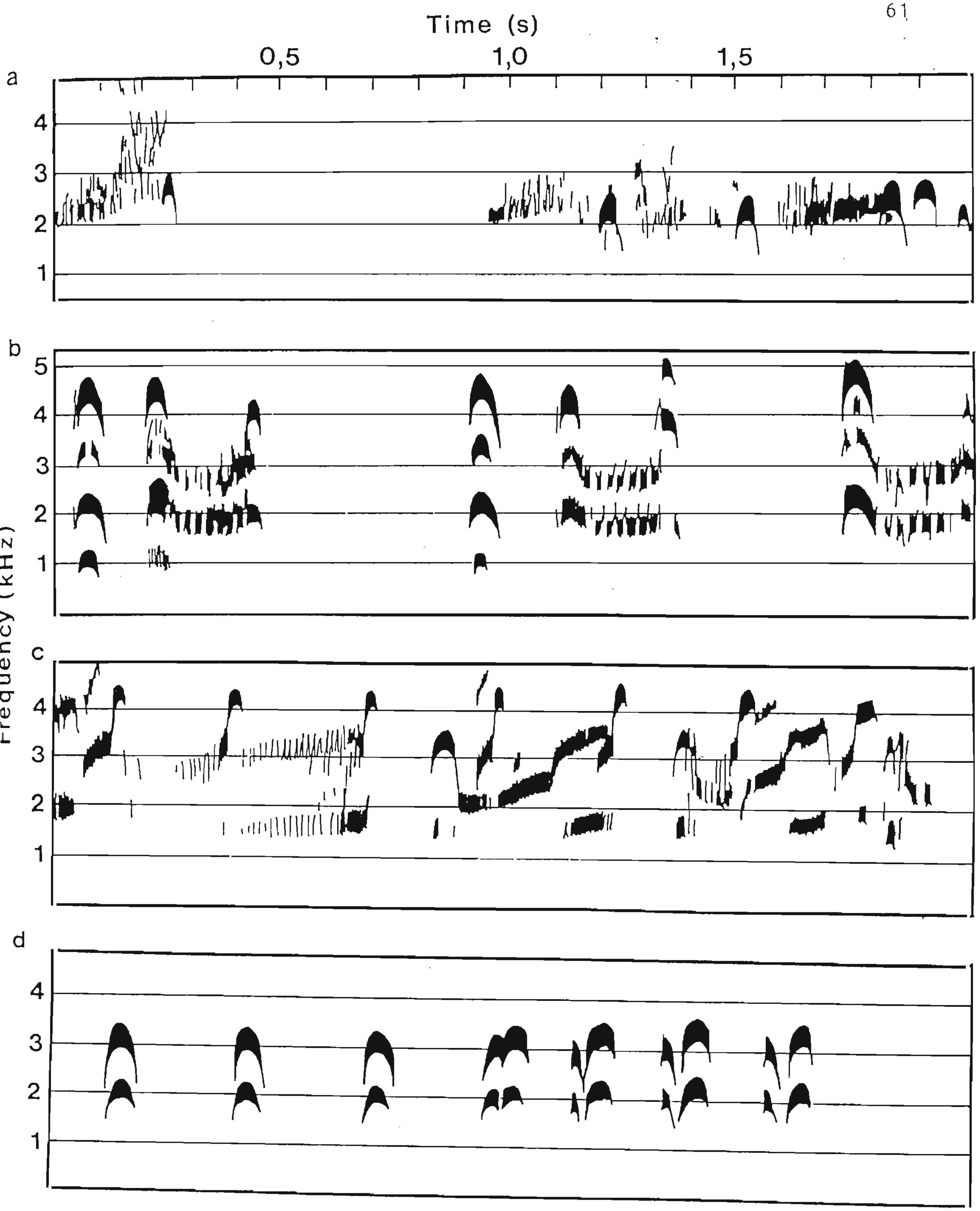

Fig. 6. Sonagrams of alarm calls of a) *Vanellus coronatus*, b) *V. melanopterus*, c) *V.armatus*, d) *V.senegallus*. The "inverted U" note is found in all of these species calls.

plover Vanellus lugubris does not respond to crowned and blackwinged plover alarm calls, apparently because the lesser blackwinged plover has different alarm-call notes (Fig. 6e) from those of other vanelline plovers and therefore does not respond to these other species' calls.

It is apparent that both species may derive benefits from this association. How then might such a behavioral association develop?

Examination of the niches occupied by some other vanelline plovers and the effects of their niches on their behaviour, shows, for example, that blacksmith plovers and longtoed plovers V. crassirostris are waterside birds and that both these species maintain territories year-round (Hall 1964; Walters 1980). They exclude all other vanelline plovers by aggressive behaviour (Maclean 1972; Walters 1980). In a natural situation (unlike at the Scottsville Racecourse where the grass is maintained, by weekly mowing, at a suitable length for prey detection), crowned and blackwinged plovers do not maintain territories all year, because the grasslands in which they live do not remain suitable for prey detection all year. As a result, these birds have adopted a nomadic existence, moving when the grass grows too long or when prey availability drops to a level at which it is no longer profitable to search for it.

It appears that crowned and blackwinged plovers have developed an

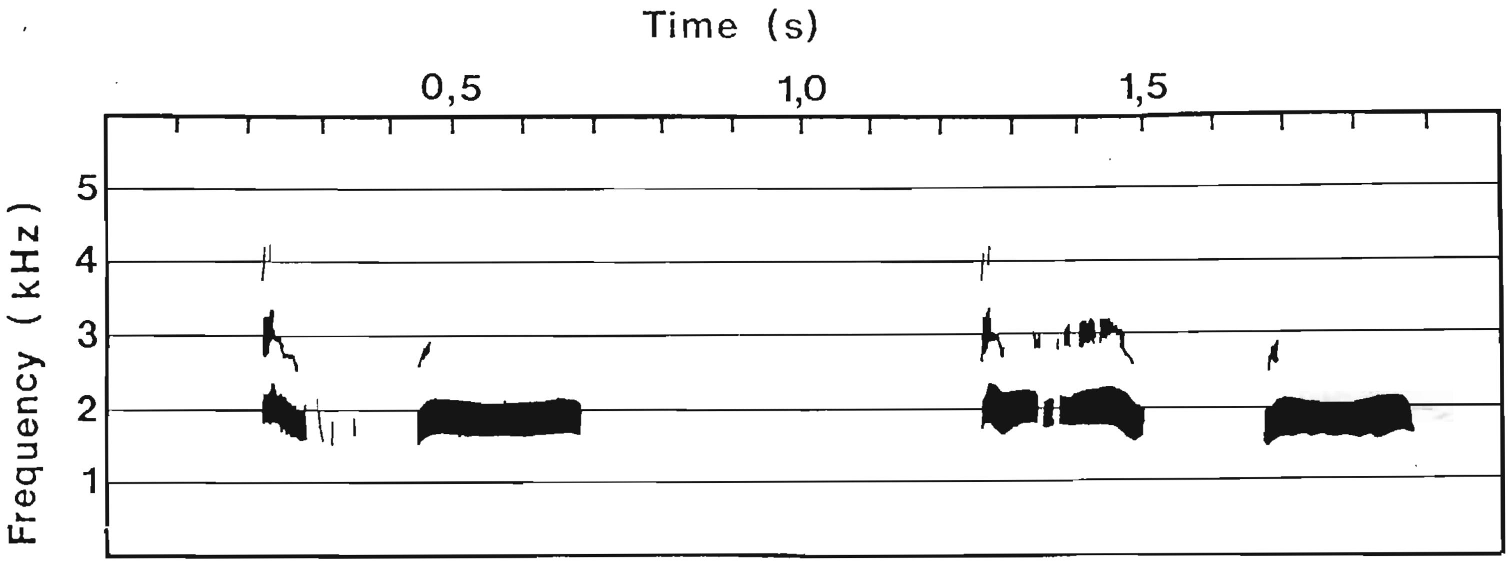

Fig. 6e. Sonagram of alarm call of Vanellus lugubris. The "inverted U" note is absent.

association as a result of the breakdown of territoriality because of changes in habitat. In cases where the habitat is artificially maintained these two species retain their association and, in certain instances, maintain territories together. This association allows crowned plovers to increase their foraging time relative to time spent vigilant, while blackwinged plovers benefit from the aggressive behaviour of crowned plovers in chasing off predators. Also, both species probably benefit from the "confusion effect" in avoiding predation. The association between these two species occurs in spite of apparent diffuse competition for food.

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Chapter 3

FEEDING ECOLOGY

INTRODUCTION

Interspecific competition is considered by many community-ecology theorists to be a major force structuring communities (Hutchinson 1959; Schoener 1965; Cody 1974). Interspecific competition is also purported to be a cause of allopatry of closely-related species (the "ghost of competition past" hypothesis (Connell 1980)).

Blackwinged and Crowned Plovers occupy the same habitat and feed together where they concur. Blackwinged and Lesser Blackwinged Plovers are allopatric, while Crowned and Lesser Blackwinged Plovers are sympatric, although they are usually allotopic (occur in different habitats) within the area of sympatry. As a result of the distributions of the study species, at both geographical and ecological levels, emphasis in this chapter is placed on an investigation of the ecological relationships between Crowned and Blackwinged Plovers in order to determine whether interspecific competition is indeed an important factor in determining community structure and distribution of closely related species. If interspecific competition is an important factor in the ecology of these species, it may explain the allopatry between Blackwinged and Lesser Blackwinged Plovers and the allotopy of

Crowned and Lesser Blackwinged Plovers.

A study of all the cursorial insectivorous birds at Scottsville Racecourse in 1986 was undertaken in order to examine the effects of these species on each other's feeding ecology, with particular emphasis on their effects on the feeding ecology of Crowned and Blackwinged Plovers. This is an unusual grassland ecosystem because it is mown weekly, but this makes it possible to detail the effects of interspecific interactions in short-grass ecosystems over a long period of time, unlike the situation prevalent in natural grasslands where the grass seldom remains short enough for use by these birds for more than two or three weeks at a time.

SECTION I : Feeding ecology of Crowned and Blackwinged Plovers

MATERIALS AND METHODS

In addition to the methods detailed in Chapter 2, 32 Crowned Plover gizzards were obtained from the Transvaal Museum, Pretoria, and their contents examined in order to compare these with the results obtained for faecal samples of this species obtained from Pietermaritzburg and Ndumu.

The importance of different prey items was determined by quadrat sampling (Chapter 2) of food availability at Scottsville

Racecourse and Ndumu in order to relate this to faecal contents of Crowned Plovers in these areas.

Twelve Crowned Plovers (four adult males, six adult females and two immature birds) and four Blackwinged Plovers (all immature birds) were kept alone in captivity for five days before starting "cafeteria tests" (Drozdz 1975). In these tests the birds were fed *ad libitum* with separate bowls containing earthworms *Microchaetus* sp., Mealworm *Tenebrio molitor* larvae, Mealworm adults and termites *Trinervitermes* sp., to determine their preferences for these prey items, which are considered to be representative of the types of prey available to the plovers. The foods were presented in all combinations of two prey types at a time (10 replicates of each combination) as well as all prey items at once (10 replicates). Each replicated experiment was performed on a separate day. The energy content of the prey items tested was analyzed by bomb calorimetry (Horowitz 1970). Ash content was determined by the mass of the remains left after bomb calorimetry. Total nitrogen and fat concentrations of each prey type were examined using standard micro-Kjeldahl and Soxhlet apparatus, respectively, according to the methods laid out by Horowitz (1970). These analyses were carried out in order to determine whether prey preferences were correlated with nutritional value of the food items.

RESULTS

The 32 Crowned Plover gizzards examined contained a very large proportion of termites (Table 3.1). Faeces of Crowned Plovers taken from Ndumu also contained mostly termites (Table 3.2). Crowned and Blackwinged Plovers ate a high percentage of termites despite the low availability of these arthropods at Scottsville Racecourse and Ndumu (Figs 3.1 and 3.2).

All Crowned and Blackwinged Plovers kept in captivity took prey in the following order : earthworms, mealworm larvae, termites and mealworm adults. All of one prey type was consumed before taking any of the less-preferred type in each case. There was no sex or age difference in prey preference between Crowned Plovers tested. Since all Blackwinged Plovers tested were immature, sex and age differences in food preferences were not tested.

Earthworms had the lowest energy, nitrogen and fat content of all the prey types tested (Table 3.3), although they had the highest water and calcium contents.

DISCUSSION

Crowned Plovers from Pretoria ate a lot of termites as did Crowned and Blackwinged Plovers at Scottsville Racecourse and

Table 3.1. Contents of 32 Crowned Plover gizzards (n = 6086 mandibles).

Hodotermes mossambicus	25,4%	
Odontotermes badius	60,9%	Isoptera = 93,1%
Trinervitermes sp.	6,2%	
Allodontotermes sp.	0,6%	
Scarabaeidae	3,0%	
Orthoptera	0,3%	
Araneae	0,4%	
Formicidae	3,2%	

Table 3.2. Crowned Plover faecal contents, Ndumu.

May 1986 (n = 2699 mandibles)		*September 1986* (n = 1298 mandibles)	
Isoptera	97,4%	Isoptera	94,9%
Scarabeidae	1,8%	Scarabeidae	3,4%
Formicidae	0,1%	Formicidae	1,7%
Diplopoda	0,7%		

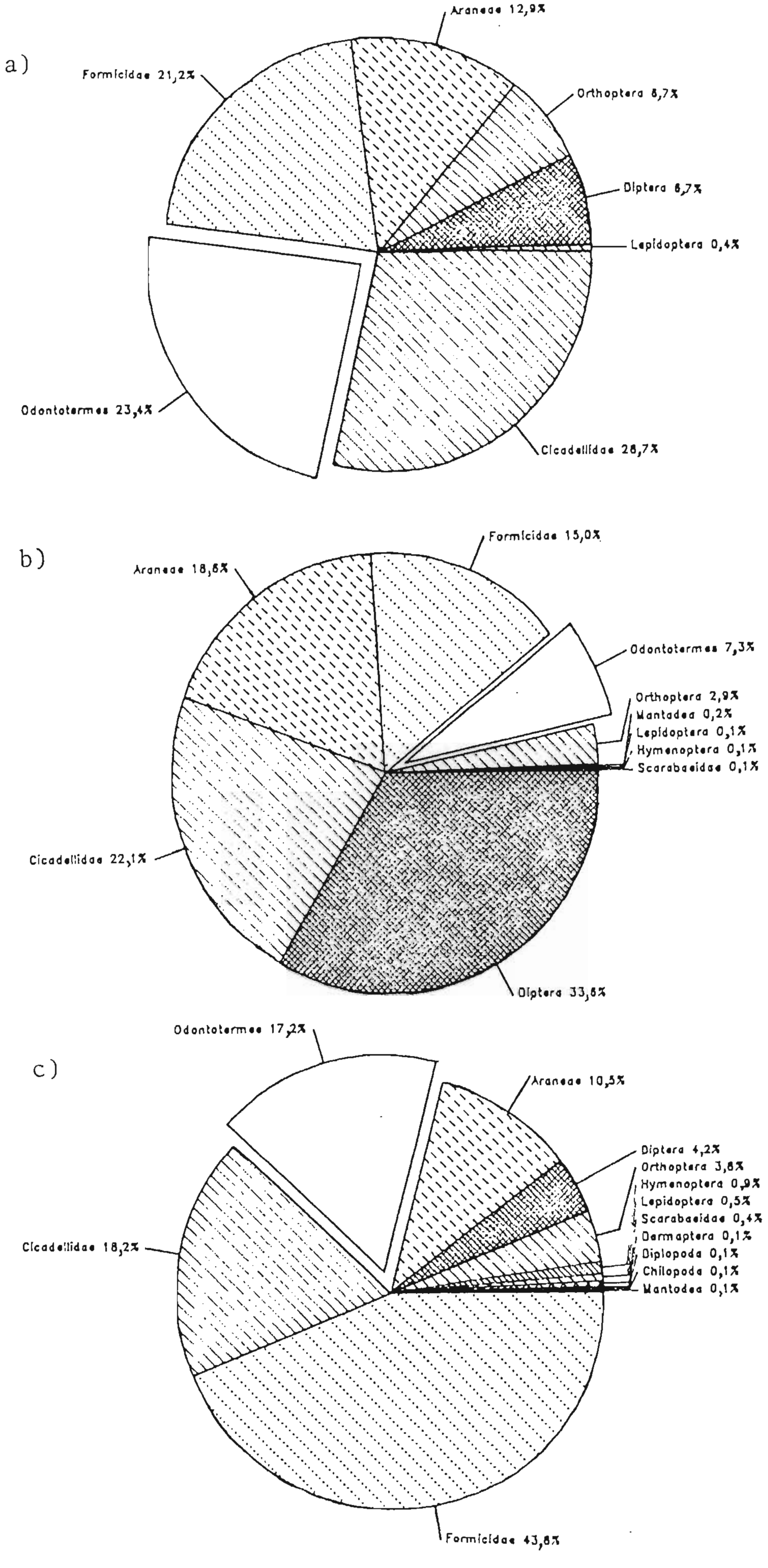


Fig. 3.1. Arthropod types available at Scottsville Racecourse in 1986.

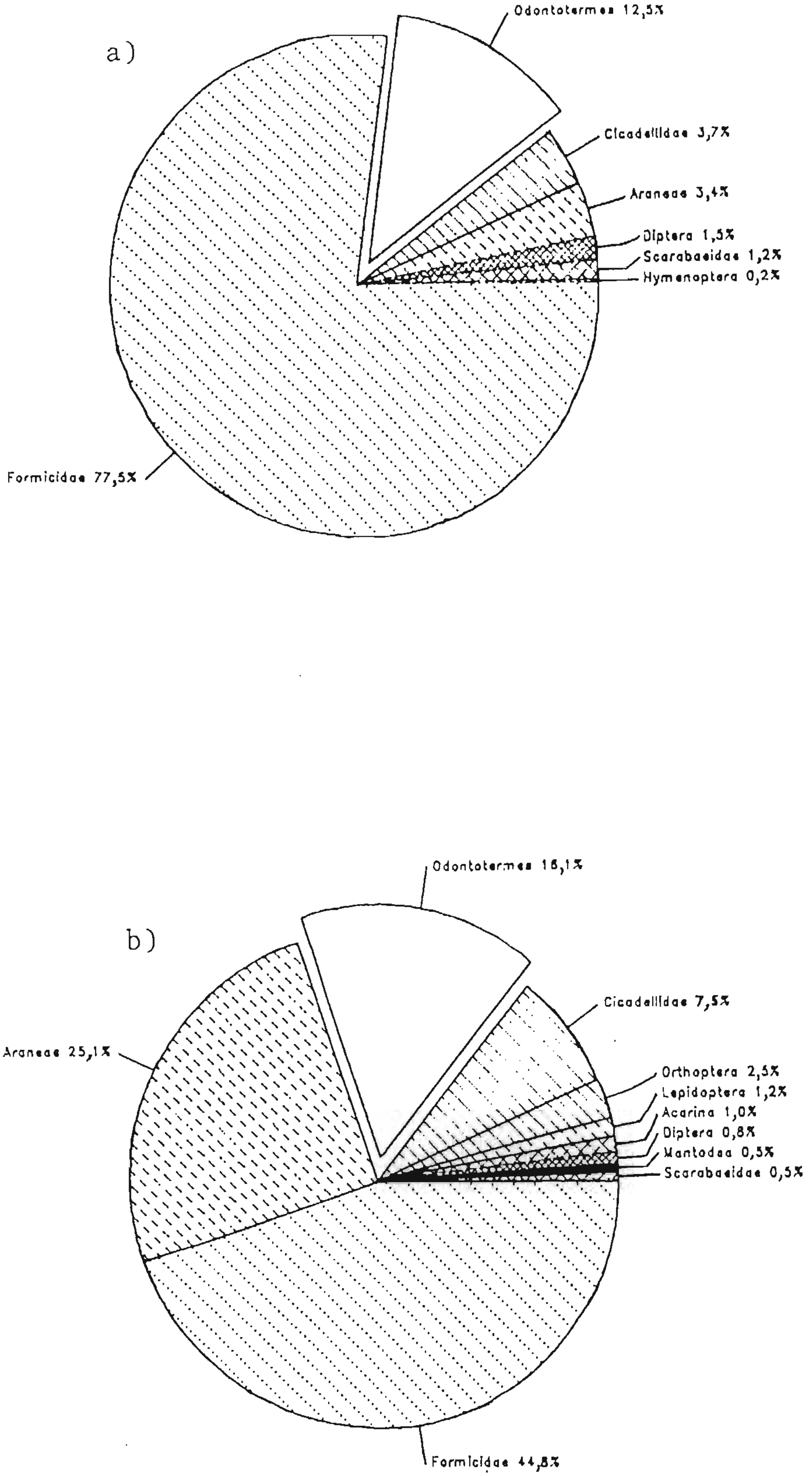


Fig. 3.2. Arthropod types available to plovers at Ndumu in 1986. (a) May-August, (b) September-December.

Table 3.3. Proximate analysis of prey items in food-preference tests.

Prey	Gross energy (MJ/kg)	Moisture (%)	Fat (%)	Protein (%)	Ash (%)	Calcium (%)
Tenebrio adults	21,70	59,50	4,50	27,09	1,29	0,01
Tenebrio larvae	26,66	57,50	16,86	19,52	1,12	0,02
Earthworms	7,12	76,22	0,43	4,23	15,83	0,25
Termites	18,00	75,00	1,98	10,69	5,00	0,19

Ndumu, despite their relative scarcity, which suggests that the birds were selecting for them. However, in food-preference tests, termites rated second-to-lowest. In terms of energy content, total nitrogen (which approximates protein content) and fat, there was very little difference between termites, mealworms and mealworm adults. It appears that termites are eaten in large quantities because they constitute a dependable resource which is easy to find, since they are found in the same place each day, while other food types are far more randomly dispersed. Termites may not be favoured in food-preference tests because soldier termites are avoided (pers. obs.) and, therefore, it takes longer for the birds to remove the prey items (worker termites). Ants are also patchily distributed but are unimportant in the diet, probably because of their formic-acid content which makes them unpalatable (Melton 1976). According to Redford & Dorea (1984), there is no difference in nutritional value between ants and other arthropods. Mealworm adults rated lowest in preference probably because of their strongly cuticularized exoskeleton which the plovers may not be able to digest. The entire exoskeleton of beetles was found in all the Crowned and Blackwinged Plover faeces examined.

Earthworms were the preferred prey item of Crowned and Blackwinged Plovers even though they are low in nutritional value. They do have a high calcium content, though, which is of value to the plovers in egg-shell development, feather growth and bone growth. Earthworms are rarely available to plovers, coming to the surface only during rain. If there is indeed a shortage of calcium in the diet of plovers, it would be advantageous for them to capitalize on earthworms whenever they were available. However, termites also have a relatively high calcium concentration and they constitute the largest portion of the diet. Earthworms are probably not selected by plovers for their water content because the plovers did not drink free water when it was available and because the earthworms are so rarely available to plovers as to be insignificant to their water balance.

A problem with all food-preference tests and tests to determine the energy/protein/carbohydrate content of prey items is that one is forced to use post hoc hypotheses to explain why animals prefer certain prey items. These hypotheses must necessarily be limited by the number of different chemical elements/compounds that you test for. Therefore, to suggest that an animal selects a certain prey item in preference to another because the former prey item has a higher concentration of a certain element than the latter would be naive. I suggest that the preference displayed by Crowned and Blackwinged Plovers for earthworms may be a result of the high calcium content of earthworms, but it may just as well be a result of the high concentration of some compound not tested for or even the fact that earthworms are bigger than the other prey items tested and the plovers eat the largest item they can see.

SECTION II : Feeding ecology of cursorial insectivorous birds at Scottsville Racecourse

MATERIALS AND METHODS

The positions of all the cursorial insectivorous birds at Scottsville Racecourse were plotted on a map of the racecourse during 10 morning and 10 afternoon feeding periods each month in 1986. These positions were used to determine the percentage similarity in habitat use of these species, as well as their degree of association. The racecourse consisted of three habitats, namely the racetrack which was watered every third day, Kikuyu Grass *Pennisetum clandestinum* areas which occurred around permanent springs and dry Couch Grass *Cynodon dactylon* areas. All three habitats were mown weekly to about 3 cm height.

Twenty Indian Mynas *Acridotheres tristis* were killed each month from May to December 1986 to determine whether their gizzard contents were similar to the gizzard and faecal contents of Crowned and Blackwinged Plovers.

RESULTS

Fig. 3.3 indicates that there were four guilds of cursorial insectivorous birds at the Scottsville Racecourse: (a) Crowned Plovers, Blackwinged Plovers, Richard's Pipits *Anthus novaeseelandiae* and Indian Mynas, (b) Hadeda Ibises *Bostrychia*

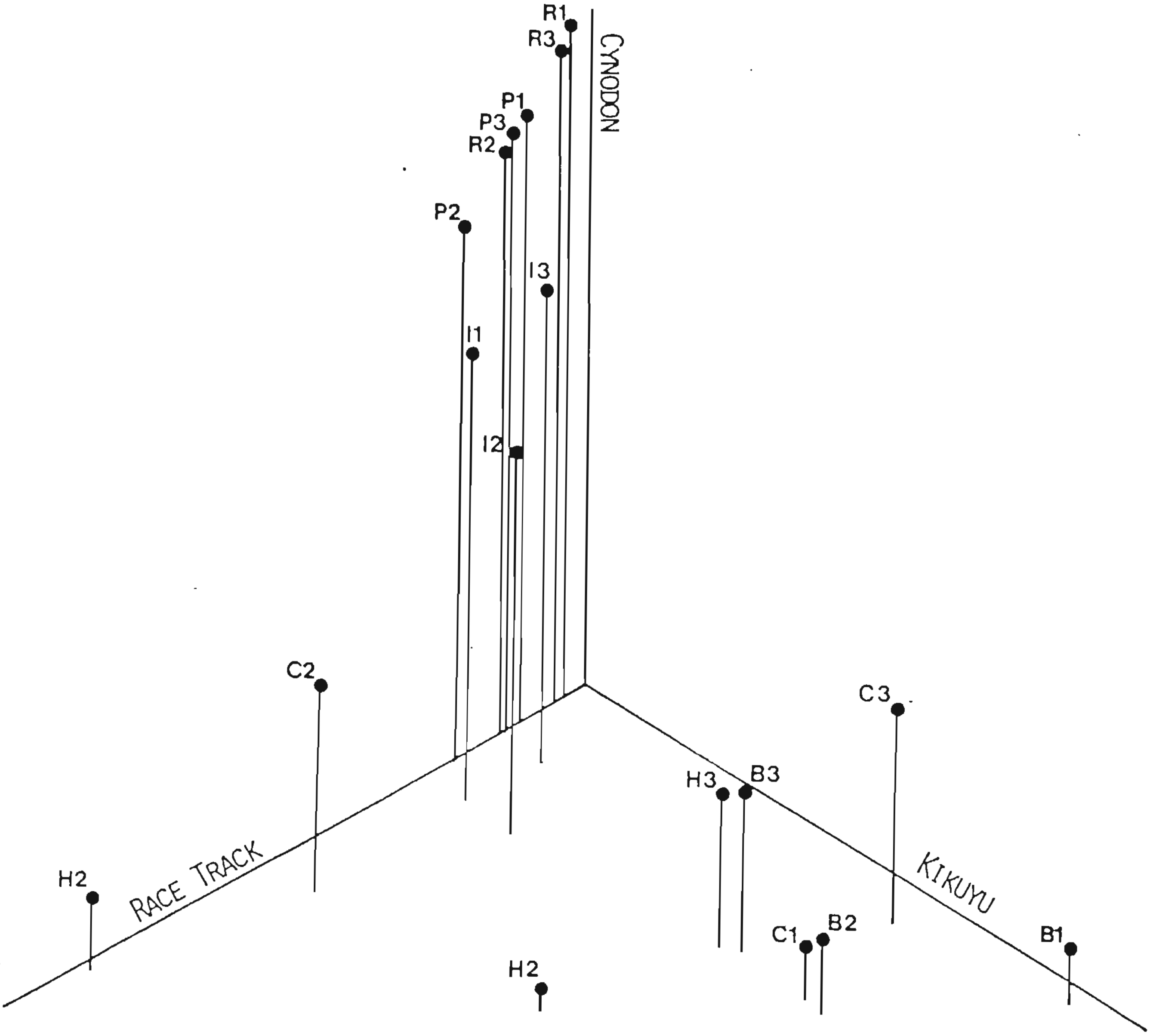


Fig. 3.3. Habitat use by cursorial insectivorous birds at Scottsville Racecourse in 1986, determined by the percentage of each species found in each habitat type. H = Hadeda Ibis; C = Cattle Egret; P = Crowned and Blackwinged Plovers; B = Blacksmith Plover; I = Indian Myna; R = Richard´s Pipit. 1 = January-April; 2 = May-August; 3 = September-December.

hagedash, Cattle Egrets *Bubulcus ibis* and Blacksmith Plovers *Vanellus armatus* in the summer periods, (c) Hadeda Ibises and Cattle Egrets in winter, and (d) Blacksmith Plovers in winter.

Indian Mynas were the only birds towards which Crowned and Blackwinged Plovers showed any aggression while feeding ($n = 127$ and 92 cases, respectively). Plovers were aggressive towards Indian Mynas when the latter species followed the plovers around looking for food. There was, however, only a low negative correlation between Crowned and Blackwinged Plover numbers and Indian Myna numbers ($r = -0{,}39$; $p > 0{,}05$; n.s.). No cases of kleptoparasitism by mynas on plovers were observed. Mynas did not usually occur in mixed flocks with plovers (12 mixed flocks were recorded in 240 censuses, involving 84 out of 5624 mynas seen). Mynas usually fed in large flocks but ran over to where the plovers were when the latter discovered a large food supply, which is when the aggression recorded above occurred. Mynas flew to where plovers were when predators appeared ($n = 77$ occasions), but did not join the plovers in mobbing the predators, rather remaining on the ground.

Gizzard contents of mynas shot at Scottsville Racecourse were more varied (Fig. 3.4) than gizzard and faecal contents of Crowned and Blackwinged Plovers but, like the plovers, also contained a large proportion of termites. Indian Mynas were opportunistic in their eating habits, as shown by six gizzards which contained only maize porridge left by humans.

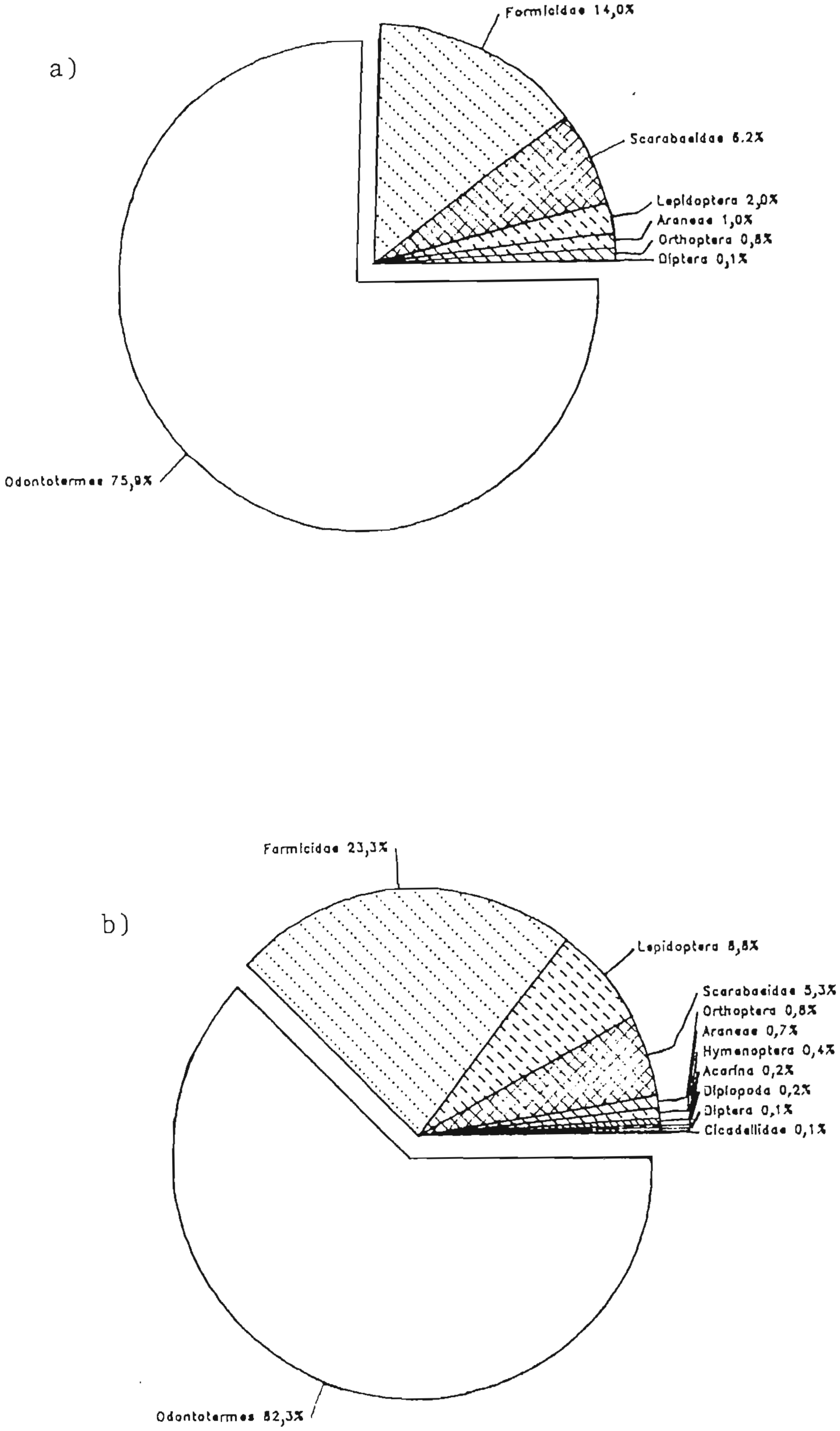


Fig. 3.4. Gizzard contents of Indian Mynas shot at Scottsville Racecourse in 1986. (a) May-August, (b) September-December.

Crowned and Blackwinged Plovers showed no aggression towards Richard's Pipits even though they fed in the same habitats. There was a low negative correlation between Crowned and Blackwinged Plover numbers and Richard's Pipit numbers ($\underline{r}$ = - 0,44; p> 0,05; n.s.). There was a low positive correlation between Richard's Pipit and Indian Myna numbers ($\underline{r}$ = 0,22; p> 0.05; n.s.). No aggression was observed between the two last-mentioned species.

DISCUSSION

Only Indian Mynas and Richard's Pipits occupied similar habitats to Crowned and Blackwinged Plovers at Scottsville racecourse. Interspecific competition for food did occur between plovers and mynas, but plovers did not act aggressively towards pipits feeding in the same areas. The lack of aggression between pipits and plovers may be a result of low prey overlap, although the diet of pipits was not investigated in this study. Borrett & Wilson (1971) found that termites were relatively unimportant in the diet of Richard's Pipits in Zimbabwe (18% of gizzards contained termites). However, pipits were observed eating termites on many occasions (positive identification on 141 occasions) at Scottsville Racecourse and may therefore compete with plovers for food on occasion. There were relatively few pipits on the racecourse, which appears to be a result of intraspecific territoriality observed ubiquitously for this species (pers. obs.), so they may remove only a small portion of the food available to plovers (especially on account of their small (±24 g (Maclean 1985)) size and, therefore, small food requirements). Plovers may, therefore, not concern themselves with aggression towards pipits which have a relatively insignificant effect on the plovers' food supply.

Indian Mynas gain two advantages from feeding near Crowned and Blackwinged Plovers: (a) defence against avian predators and (b) assistance (albeit incidental on the part of the plovers) in finding food. A possible reason for plovers' displaying aggression towards mynas, and not pipits, is that the large flocks of mynas that occur on Scottsville Racecourse may otherwise remove a significant portion of the plovers' food supply.

The insignificant correlations between Crowned and Blackwinged Plover numbers and Richard's Pipit numbers and Indian Myna numbers indicate that interspecific competition is unimportant in establishing the structure of the cursorial-insectivore community in which Crowned and Blackwinged Plovers live at Scottsville Racecourse. That is not to say that interspecific competition is not important in the relationships between the species at the racecourse at all, since interspecific competition is likely to be the cause of aggression displayed by Crowned and Blackwinged Plovers towards Indian Mynas.

SECTION III : Feeding ecology of Lesser Blackwinged Plovers

MATERIALS AND METHODS

Observations were made on the feeding ecology of Lesser Blackwinged Plovers opportunistically. Faecal samples were collected in Ndumu Game Reserve in May and September 1986. Four Lesser Blackwinged Plovers were shot in open grassland near Pelindaba, northern Natal and their gizzard contents examined.

RESULTS

Feeding Behaviour

Lesser Blackwinged Plovers feed, as do Crowned and Blackwinged Plovers, by picking prey items off the substratum and by probing into softer soils. All probing occurred after a prey item had been detected, rather than by feeling around with the bill, as is the case with scolopacid waders which detect prey items by touch rather than by sight (Johnsgard 1981). Lesser Blackwinged Plovers also removed prey items from beneath the soil surface by kicking soil backwards with their feet, one foot at a time. This last-mentioned behaviour was not seen in Crowned or Blackwinged Plovers.

Prey

The gizzards of four Lesser Blackwinged Plovers and faecal samples obtained in May and September 1986 indicate (Table 3.4) that prey items taken by Lesser Blackwinged Plovers are similar to those taken by Crowned Plovers at the nearby Ndumu Estates (Table 3.2). The preference of Lesser Blackwinged Plovers for termites is indicated by the far higher proportion of these insects in the diet than in prey available (Fig. 3.2).

Feeding associations

Lesser Blackwinged Plovers foraged in woodlands with Crowned Plovers, Bushveld Pipits *Anthus caffer*, Sabota Larks *Mirafra sabota*, Flappet Larks *Mirafra rufocinnamomea*, Glossy Starlings *Lamprotornis nitens*, Forktailed Drongos *Dicrurus adsimilis* and Redcrested Korhaans *Eupodotis ruficrista*. The only aggression observed in 230 h was seven cases of kleptoparasitism by Forktailed Drongos on Lesser Blackwinged Plovers. Lesser Blackwinged Plovers also foraged with Glossy Starlings, Pied Barbets *Lybius leucomelas*, Rufousnaped Larks *Mirafra africana*, Sabota Larks, Flappet Larks and Bushveld Pipits at rhinoceros middens without interspecific aggression being observed in 43 h. On cultivated lands Lesser Blackwinged Plovers foraged with Hadeda Ibises *Bostrychia hagedash*, Cattle Egrets *Bubulcus ibis*, Pinkthroated Longclaws *Macronyx ameliae*, Orangethroated Longclaws *M. capensis*, Yellowthroated Longclaws *M. croceus*, Kittlitz's

Table 3.4. Lesser Blackwinged Plover prey items.

a) Faecal contents:

May 1986 (n = 1896 mandibles)		September 1986 (n = 1727 mandible	
Isoptera	89,0%	Isoptera	75,2%
Scarabeidae	5,6%	Scarabeidae	13,4%
Formicidae	3,3%	Formicidae	4,5%
Araneae	0,7%	Araneae	4,5%
Diplopoda	1,4%	Orthoptera	2,5%
		Diplopoda	0,9%

b) Gizzard contents of four birds (n = 1389 mandibles):

Isoptera	58,5%
Lepidoptera larvae	33,3%
Orthoptera	4,7%
Araneae	3,5%

Plovers *Charadrius pecuarius*, Caspian Plovers *C. asiaticus*, Crowned Plovers, Blacksmith Plovers *Vanellus armatus*, Wattled Plovers *V. senegallus* and Ruffs *Philomachus pugnax*, without interspecific aggression being observed in 35 h. Lesser Blackwinged Plovers associated with Wattled Plovers at muddy edges of two pans without interspecific aggression in 13 h of observation. Lesser Blackwinged Plovers fed in burnt areas alongside Crowned Plovers, Temminck's Coursers *Cursorius temminckii*, Ruffs and Richard's Pipits *Anthus novaeseelandiae* without interspecific aggression being observed in 27 h. Lesser Blackwinged Plovers foraged alongside Crowned Plovers in open woodland at Ndumu Estates with three cases of interspecific aggression observed in 32 h of observation. In all three cases of aggression, a pair of Crowned Plovers chased off four Lesser Blackwinged Plovers which ventured within 5 m of the former's nest.

DISCUSSION

Lesser Blackwinged Plovers were opportunistic in their choice of feeding habitat, using any habitat where the vegetation was short or absent. Interactions between this species and other insectivorous birds were rare and may result from the opportunistic use of habitat, the birds concentrating on behaviour that maximize food intake over a short period of time, moving to other feeding areas as soon as prey availability drops to levels at which it is no longer profitable to search for it.

Lesser Blackwinged Plovers bred in open woodlands where there were no other diurnal, cursorial insectivorous birds. All other birds seen feeding with Lesser Blackwinged Plovers were either opportunistically using this habitat (larks and korhaans) or were arboreal insectivores which opportunistically fed on the ground, so overlap of prey use was likely to be small.

GENERAL DISCUSSION

A feature common to the feeding ecology of Crowned, Blackwinged and Lesser Blackwinged Plovers is the lack of interspecific aggression between these species in spite of overlap in the foods they eat. A similar lack of aggression between birds of short grasslands has been found by Cody (1985). Baldwin (1973), Maher (1979) and Wiens & Rotenberry (1979) have shown that a strong overlap in diet is typical among different grassland bird species at the same site, that common food items may vary from year to year and that interspecific dietary overlaps may likewise vary between years. Wiens & Rotenberry (1980) found only weak correlations between culmen morphology and diet and emphasized the opportunistic nature of foraging grassland birds. In shortgrass vegetation, body sizes of birds are more variable than in long-grass vegetation and culmen morphologies are less uniform than in other vegetation types (Cody 1985), supporting the notion that relationships between species are not regimented in short *morinellus* (Thompson & Thompson 1985) and between European Lapwings and Greater Golden Plovers *Pluvialis apricaria* (Thompson & Barnard (1983). It is likely that these relationships have developed as a result of the high predation pressures on birds living in exposed habitats and the lack of interspecific territoriality which has developed as a result of the transient nature of these grasslands causing these birds to move when the habitat becomes unsuitable.

Chapter 4

BREEDING BIOLOGY

INTRODUCTION

Like all *Vanellus* species, Crowned, Blackwinged and Lesser Blackwinged Plovers are ground-nesters. The three study species nest in areas of short or burnt grass in open grasslands or open woodlands far from water bodies, usually during winter or early spring. Nests of these species are scrapes on the ground and have no cover to shield the birds from the elements while incubating. One of the aims of this study was to examine the adaptations of these species to exposure of the incubating adults, as well as their eggs and chicks, to insolation. A study of the incubation regimes of these three species is important because virtually all previous studies of ground-nesting birds in hot environments have been restricted to species nesting near water and the use by these species of water to decrease egg temperatures during hot periods (*e.g.* Jayakar & Spurway 1965, Howell 1979, Grant 1982). The exceptions to this are the studies of Maclean on the Doublebanded Courser (1967) and Australian Pratincole (1976).

In addition, the behaviour of these species in mate and territory acquisition and defence was documented and related to the effectiveness in the habitats these birds occupy. The behaviour mentioned in this chapter will be related to phylogeny in Chapter 6. The openness of the habitat occupied by vanelline plovers makes them particularly vulnerable to predation and, as a result, they have a highly-developed ability to detect potential predators and and have developed a number of behavioural strategies to avoid predation (Walters 1980), which will be documented here with specific reference to effects of predation on reproductive success.

Aspects of the breeding biology of Crowned, Blackwinged and Lesser Blackwinged Plovers pertaining to life-history patterns are documented in Chapter 5.

MATERIALS AND METHODS

The behaviour of colour-marked Crowned, Blackwinged and Lesser Blackwinged Plovers was observed in the field. The behavioural patterns of these three species of plover are very similar and so will be discussed as one, noting where they differ.

Plovers were caught on the nest using a wire trap described by Sordahl (1980). Birds were individually marked using different combinations of colour bands placed on their tibiotarsi.

All eggs found were measured using Vernier calipers across the length and greatest breadth of the shell. These measurements were used to derive a measure of egg volume using Hoyt's (1979) formula $\underline{V} = 0,51 \times \underline{L.B}^2$. Clutch size was analyzed using data from field observations and from nest-record cards collected by the South African Bird-ringing Unit (SAFRING) at the University of Cape Town.

Incubation was studied in one pair of Crowned Plovers in Pietermaritzburg and three pairs of Crowned Plovers at Ndumu Estates, three pairs of Blackwinged Plovers in Pietermaritzburg and three pairs of Lesser Blackwinged Plovers in Ndumu Game Reserve. Incubation temperatures were measured mostly during the day, as well as for a single night period (18h00 - 06h00) at each nest. Incubation temperatures were measured using a YSI model 401 telethermometer placed in a hide 10 m from the nest. Three probes running from the telethermometer to the nest were placed between the eggs on the floor of the nest (to measure nest-air temperature), on the top of a false plaster-of-paris egg painted to resemble a plover egg (to measure brood-patch temperature), and 1 m from the nest and raised 5 cm above the ground (to measure ambient temperature experienced by the bird), respectively (Fig. 4.1). The difference between brood-patch and nest-air temperatures demonstrates the gradient in temperature between the top and bottom of the eggs. Wind speed was measured using a hand-held anemometer.

Sonagrams of plover calls were produced using a Kay 7029A sonagraph with a wide-band filter (300Hz).

Crowned and Blackwinged Plover chicks were colour-banded, weighed

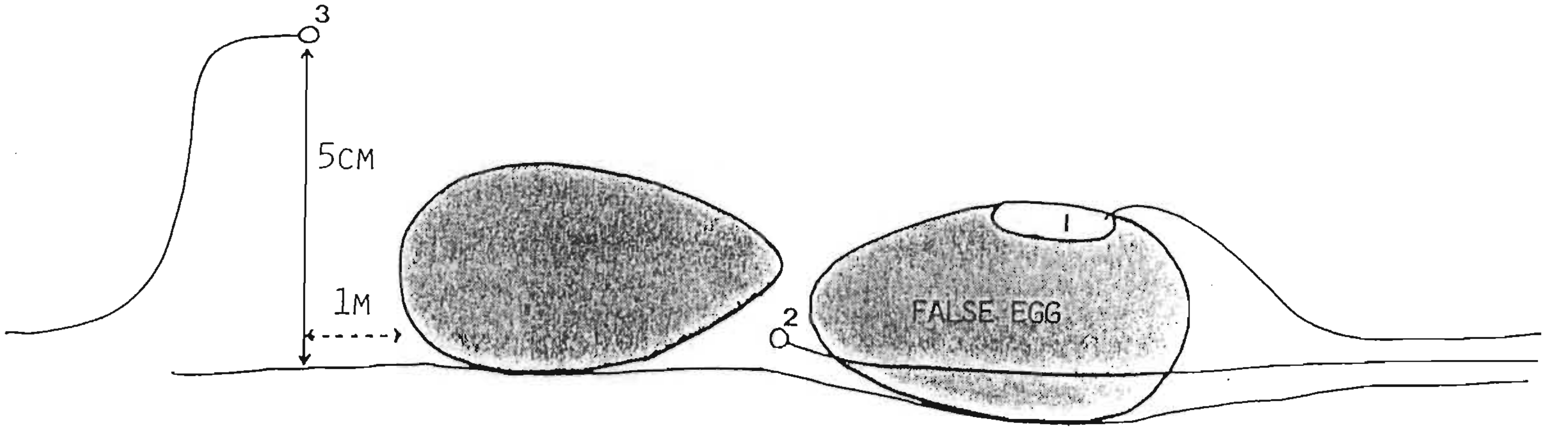


Fig. 4.1. Schematic diagram of probes used to determine incubation temperatures in plover nests (side view). 1 = brood-patch probe; 2 = nest-air probe; 3 = ambient temperature probe.

and measured daily, where possible, to determine growth rates. Because of their cryptic coloration, it was not always possible to find each chick each day, so a growth curve was constructed using combined weights and measurements of different chicks.

RESULTS

Acquisition of mates and territories

In 1985 and 1986 Crowned and Blackwinged Plovers showed increasingly aggressive behaviour from the beginning of April, males starting to fight with one another and established pairs copulating frequently. This aggressive behaviour was concomitant with a change in colour in both species. Crowned Plovers developed a deeper red on the legs and the base of the bill. Blackwinged Plovers, which lose the red eyering colour and have duller red legs and less black in the breastband during the post-breeding period, regain these characters. Lesser Blackwinged Plovers did not undergo any behavioural or plumage changes until immediately before breeding, when unpaired males begin to solicit mates.

Crowned, Blackwinged and Lesser Blackwinged Plovers acquired mates first by establishing a territory and then by soliciting females. Acquisition of territory began with the male calling, usually from a raised area such as a termite mound in the early morning and evening (a repetitive <u>kweep-kweep</u> call (Fig. 4.2c)

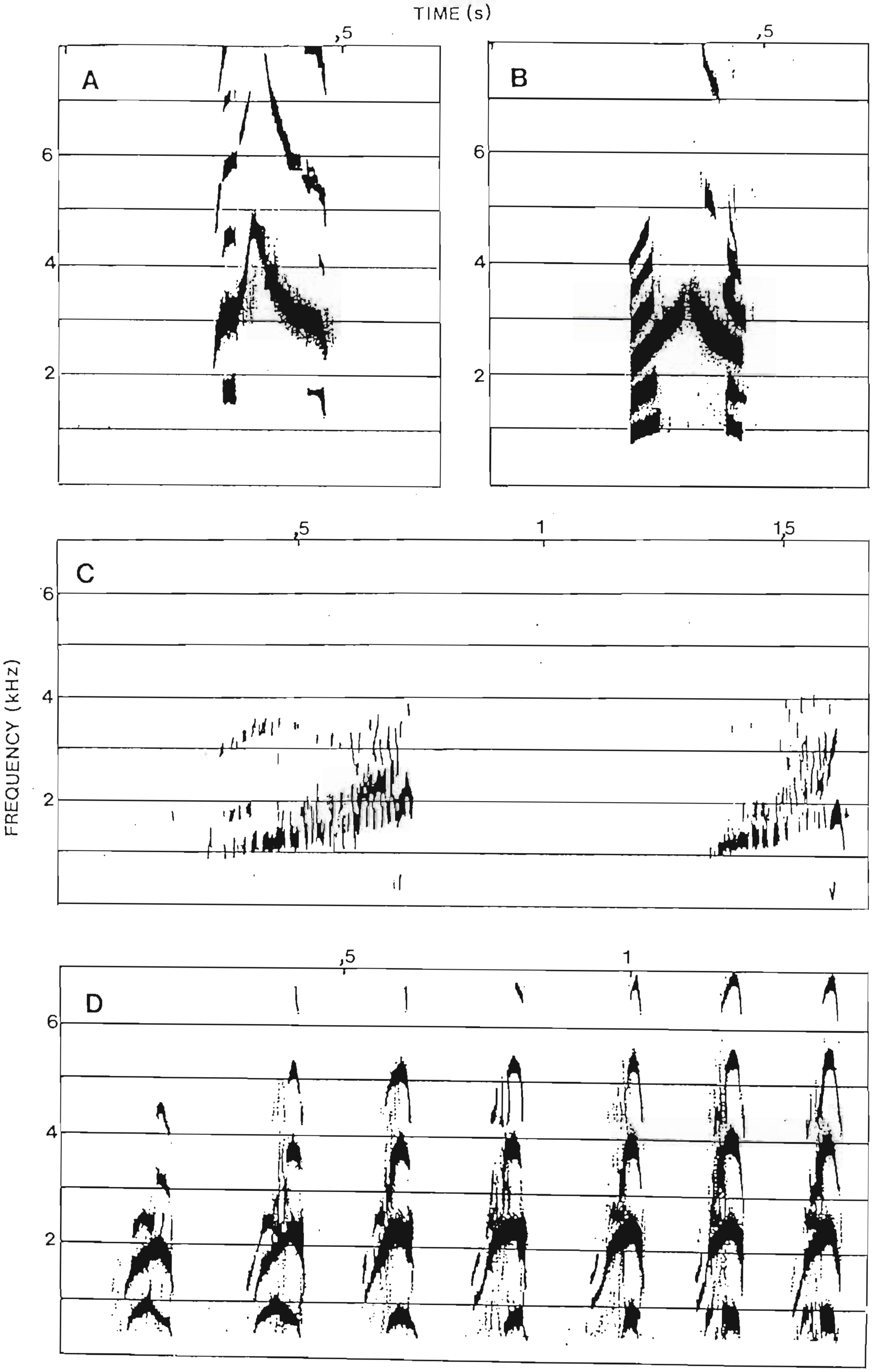


Fig. 4.2. Sonagrams of Crowned Plover calls: (A) downy chick, (B) 30-day old chick, (C) low-intensity call (adult), (D) high-intensity call (adult).

which increased in intensity in Crowned Plovers, a continual tiree-tiree-tiree call (Fig. 4.3a) in Blackwinged Plovers and a mournful ti-uh-huh call (Fig. 4.3c) repeated once every 2-3 s in Lesser Blackwinged Plovers). This calling was followed by a circular flight at 50 m above the ground (about 100 m in Lesser Blackwinged Plovers) of about 500 m diameter. This flight, in the case of Crowned and Blackwinged Plovers, consisted of the "butterfly flight" (Dabelsteen 1978) with deeply exaggerated wingbeats. This was followed after about 3 s by the "alternating flight" (Dabelsteen 1978) which involved the "butterfly flight" but the body and wings were tilted alternately from side-to-side so that the bird banked up to 45° from the horizontal. The calls mentioned above were repeated throughout the circular flight. Lesser Blackwinged Plovers performed the circular flight without exaggerated motion of the wings, and called throughout the flight as they did before the flight. Female plovers then indicated their choice of male by flying up to join them and following them in the circular flight (in "butterfly" and "alternating" flights in the case of Crowned and Blackwinged Plovers). In all three species, the female flew 1-3 m behind and about 1 m to the side of the male. Descent from the circular flight was rapid and occurred directly above the territory, the birds descending within the space of 15 m in a spiral path.

Upon alighting, Crowned Plovers made a witta-witta-witta call (not tape-recorded), Blackwinged Plovers a tiree-tiree call (Fig. 4.3a) and Lesser Blackwinged Plover males continued the ti-uh-huh

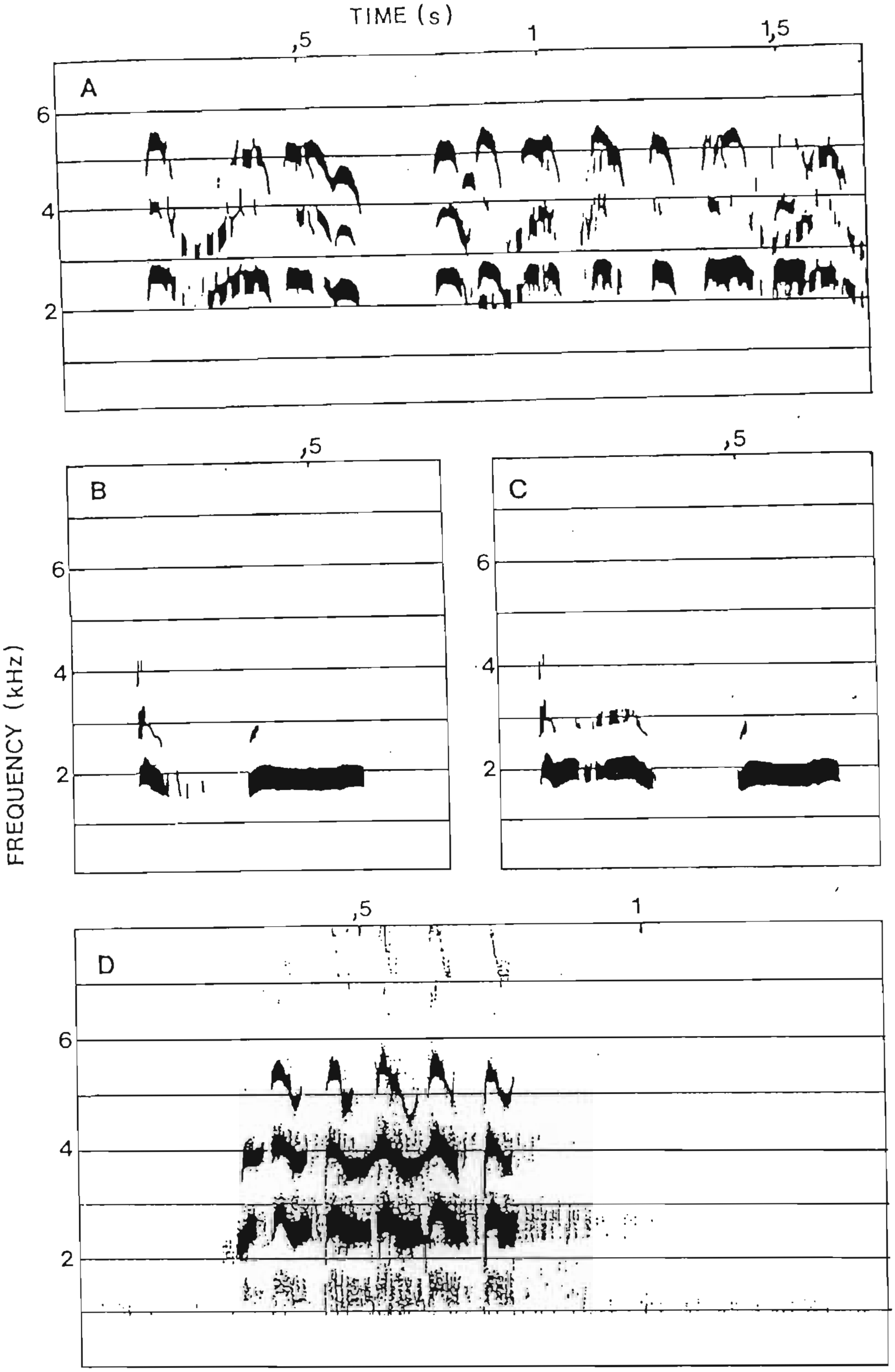


Fig. 4.3. Sonagrams of: (A) Blackwinged Plover territorial call; (B) Lesser Blackwinged Plover territorial call; (C) Lesser Blackwinged Plover display call; (D) Lesser Blackwinged Plover call performed when taking flight.

call. Thereafter, in each species, the female moved up to the male, thrust her head forwards within 2 cm of his face and then walked swiftly away from him for about 3 m and squatted down. The male then mounted and copulation ensued. The pair then stood up, the male alongside and to the right of the female with his right wing raised vertically, the hand closed, while the female did the same with her left wing (Crowned Plover and Blackwinged Plover; although in the latter species the pair ran for about 1 m while performing the display). Lesser Blackwinged Plovers had no post-copulatory display but had a vocal display during copulation (a low trew-trew call (not tape-recorded) was emitted by the male while he pointed his bill down towards the female, while she leant her head back to face him).

Competition between males for females occurred on the ground, at a focal point of raised ground (usually a termite mound or a rock). The competitors chased one another off the focal point by threat displays (Fig. 4.4), in which the head was drawn in towards the body and the neck feathers were ruffled, while the wings were drooped so that the white of the belly could be seen from the side between the joint of the radius and carpals and the chest. A bird signalled defeat by either putting its head down and lifting the wing that was further away from the aggressor upright with the hand closed (Crowned and Blackwinged Plovers) or by lifting both wings with folded hand. Crowned and Blackwinged Plovers also showed threat by lifting both wings vertically, with open hands, and making a slight jump (usually about 2-3 cm high),

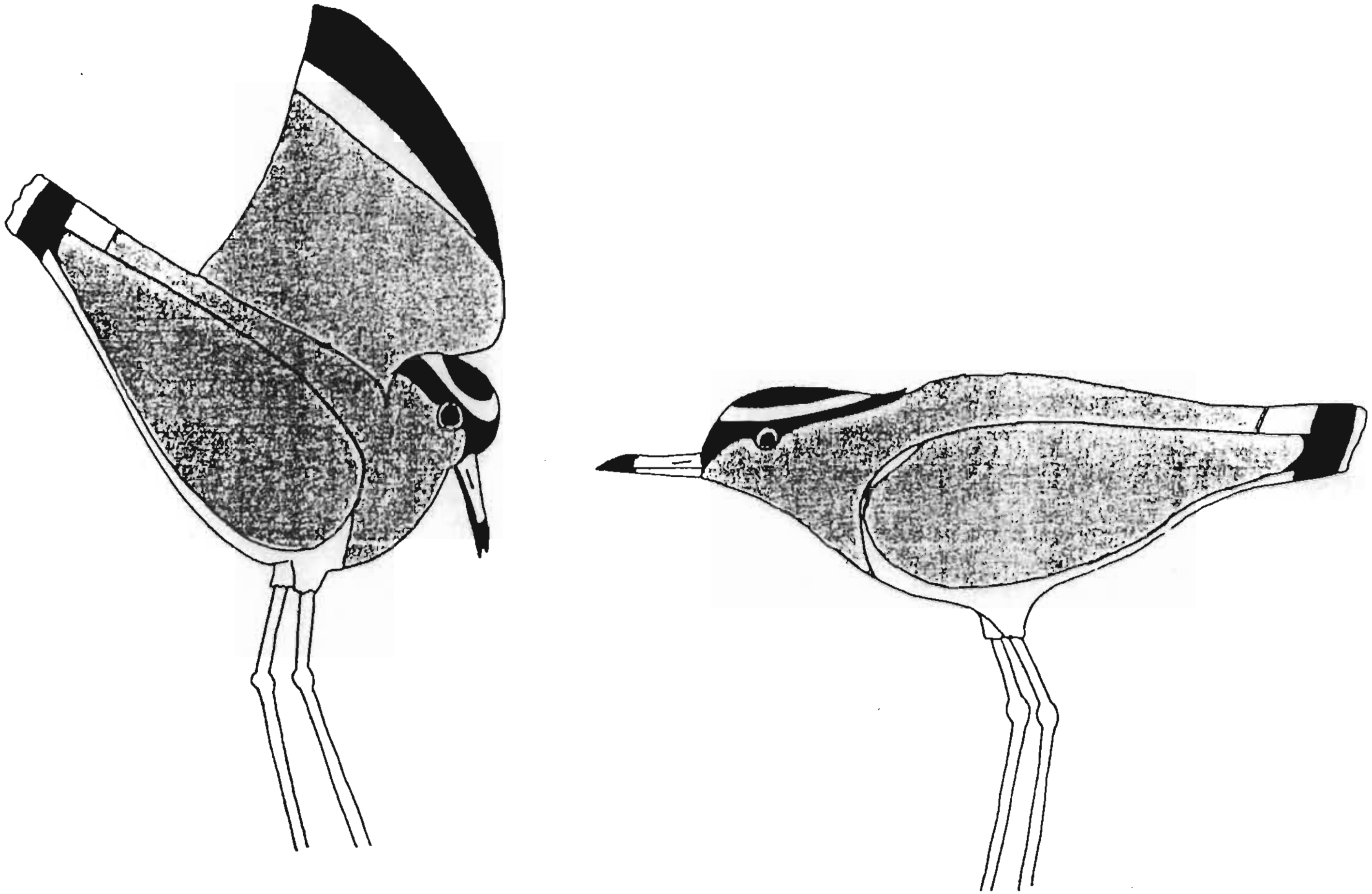


Fig. 4.4. Crowned Plover territorial defence. The bird on the right is in the aggressive threat posture, while the bird on the left (the intruder) signals submission by lifting its wing.

although they occasionally jumped right over an aggressor. Competition between males for mates also occurred during the circular flight over the territory, where the aggressor flew behind the territory owner and moved from side-to-side of the front bird, vocalizing continually. The contest was then continued on the ground in the manner described above.

Eleven male Crowned Plovers retained the same partner over the entire study period. No Crowned Plovers changed partners over this period. Of the three marked Lesser Blackwinged Plovers that returned to breed in Ndumu in 1986, none had the same partner as the previous year. No paired adult Blackwinged Plovers were marked in 1985 so mate retention could not be observed.

Territorial defence took a number of forms. It occurred either in the same manner as male-male competition for mates or in a more passive form in which the male territory owner either stretched his body to its full length and then bobbed his whole body backwards (all three species), or bobbed the neck upwards with virtually no body movement (Lesser Blackwinged Plover only). Both forms of bobbing were accompanied by a downward flick of the tail. The intruding bird indicated submission by a sideways flick of the tail (this sideways flick also occurred when a bird joined a roosting flock in the nonbreeding period). The Lesser Blackwinged Plover had another passive display in which the territory owner vigorously ruffled up all its body and head feathers and then shook its body from side to side, this vibration producing a <u>vrip</u> sound as the display was terminated. Submission was shown by a sideways flick of the tail.

Young Crowned Plovers of the previous season also assisted in territorial defence in those cases where they had not left the parents to set up their own territories. Juvenile Crowned Plovers were allowed to stay with their parents in Ndumu only when they were members of the first brood of the year (<u>i.e.</u> they were not yet a year old when the clutch of the following season was laid).

Eight pairs of marked Crowned Plovers bred in the same territories in 1985 and 1986 (five of these pairs were in Ndumu and bred in the same territories three times in two years). Crowned Plovers bred in the same territories only where these were maintained by mowing or overgrazing. Only one pair of marked Lesser Blackwinged Plovers nested in the same territory in 1985 and 1986. No paired adult Blackwinged Plovers were marked in 1985.

All Crowned and Blackwinged Plovers a year old and older bred in the study areas in 1985 and 1986. All Lesser Blackwinged Plovers in Ndumu in 1985 bred, while in 1986 28 Lesser Blackwinged Plovers arrived in Ndumu yet only 16 paired up and produced clutches of eggs. Three Crowned Plovers (two males and one female) produced young in separate pairings when still 12 months old, while one Blackwinged Plover female and one Lesser Blackwinged Plover female nested when only 12 and 13 months old, respectively. All these birds produced offspring which survived to flying age, although the Crowned Plover female produced one clutch which was eaten by a Gymnogene *Polyboroides typus*. The second clutch of three eggs laid by this Crowned Plover (initiated four days later) was successful, all three young surviving to flying age.

Nest-site selection

Discussion of the nesting habitats occupied by the study species can be found in Chapter 1. Selection of nest sites within these habitats is similar in Blackwinged and Lesser Blackwinged Plovers since both species preferred burnt areas to any other. Where burnt areas were available these two species used them exclusively. However, Blackwinged Plovers also nested in grass of 8-15 cm length and 100% basal density (two nests), while Lesser Blackwinged Plovers never nested in grass more than 5 cm tall. Crowned Plovers display a preference for unburnt areas (only nine out of 51 nests were on burnt ground - where short and burnt ground was available, they always nested on unburnt grass). Vegetation density in the vicinity of the nest (50 x 50 cm area around the nest) varied from 0-70% in Crowned Plovers (x = ±40%; n = 51 nests), 0-60% on burnt areas (x = ±40%; n = 19 nests) and 100% on unburnt areas in Blackwinged Plovers, and 0-50% in Lesser Blackwinged Plovers (x = ±30%; n = 33 nests).

All Blackwinged Plover nesting sites were placed on the tops of slopes. Crowned Plovers nesting in the same geographic area as Blackwinged Plovers (i.e. Pietermaritzburg) showed no preference for tops of slopes (only 13 out of 51 nests were on the tops of slopes). Seven Blackwinged Plover pairs nested within 1 m of a rock or raised object (e.g. a log or bush) about the size of the bird (±10 cm tall). Only one Lesser Blackwinged Plover pair and no Crowned Plovers nested near raised objects.

All three species usually nested in loose colonies, the largest for each species being 17 pairs (Crowned Plovers), and seven pairs (both Blackwinged Plovers and Lesser Blackwinged Plovers). Where these birds nested in adjacent territories, the mean ±S.E. distances between nests were 76,23 ±8,45 m for Crowned Plovers, 81,56 ±10,88 m for Blackwinged Plovers and 56,48 ±10,55 m for Lesser Blackwinged Plovers. Three mixed colonies of Crowned and Blackwinged Plovers were found (Chapter 2 - Fig. 5). Spotted Dikkops *Burhinus capensis* were found nesting in adjacent territories to all three plover species at Pietermaritzburg and Ndumu, while Redwinged Pratincoles *Glareola pratincola* and Temminck's Courser *Cursorius temminckii* nested in adjacent territories to Crowned Plovers at Pelindaba. No interspecific aggression was observed between any of these species at any of the colonies. Six pairs of Redeyed Doves *Streptopelia semitorquata* nested in the trees that were closest to each of six Lesser Blackwinged Plover nests.

Nest construction

Nests of all three species were shallow scrapes in the ground about 4 cm deep excavated by both male and female by lying on their breasts and scratching out the soil by kicking out backwards with the feet. As incubation progressed, the nests were filled with nesting material, by sideways-throwing behaviour described below. Nest material served to make the nest cryptic and consisted mostly of short pieces of grass 2-3 cm long, although small stones, moss and antelope droppings were frequently used. Blackwinged Plovers nesting in longer, unburnt grass, used no lining. All pairs of the three study species made several scrapes within the territory although only one was ever used by each pair for egg-laying.

Initiation of egg-laying

Crowned Plovers and Blackwinged Plovers in Pietermaritzburg started laying in August 1985. Rain only fell in September 1985 (Fig. 4.5), bringing with it flushes of the phytophagous insects that the birds feed on. There was no change in mean maximum temperature between July and August 1985 although the mean minimum temperature rose from July to August 1985 (Fig. 4.6). In 1986, Crowned and Blackwinged Plovers started laying in late July and August. Again, this laying activity preceded the rains (Fig. 4.7) and was concomitant with an increase in mean minimum temperature from July to August 1986 (Fig. 4.6). The dates of

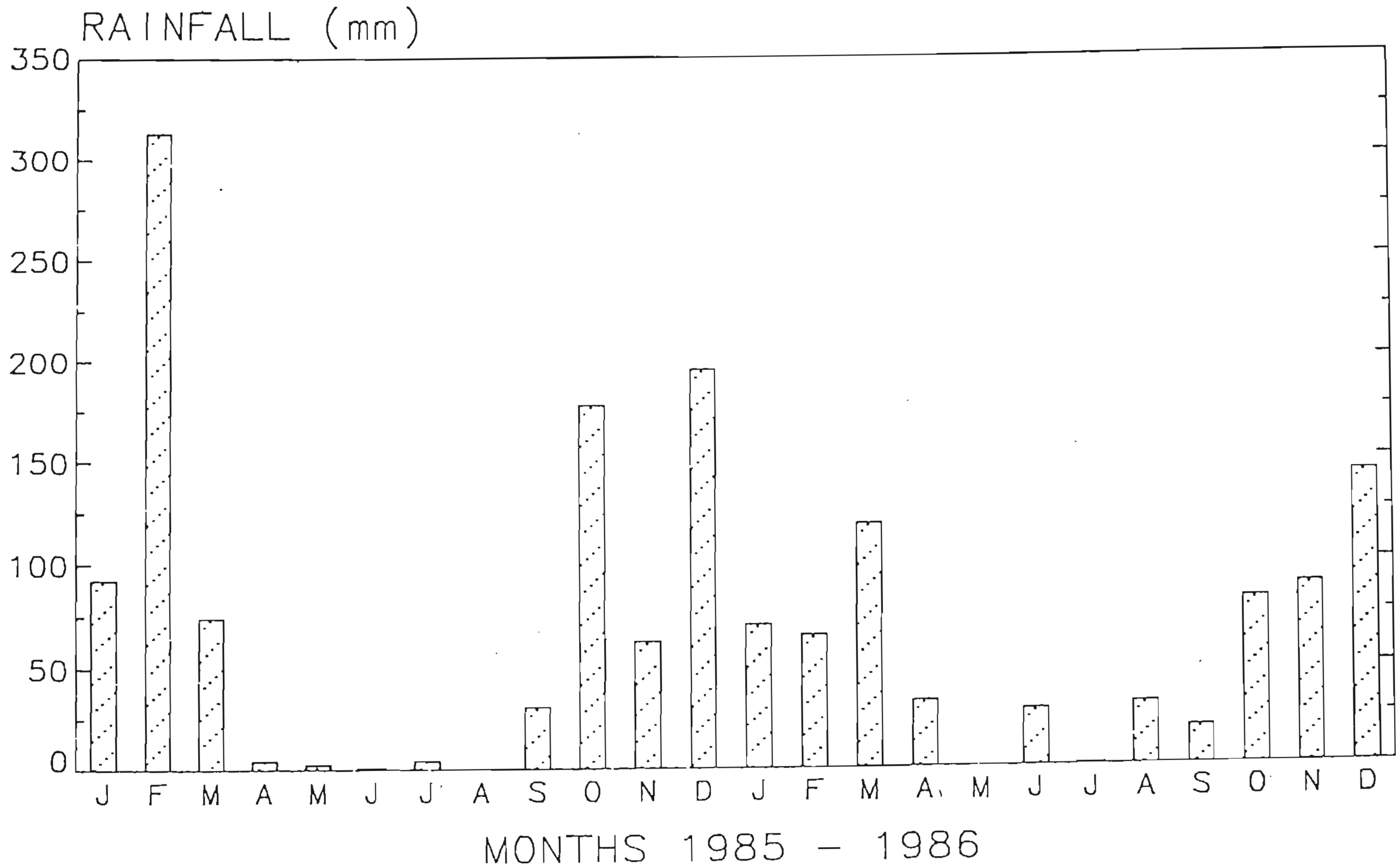


Fig. 4.5. Rainfall in Pietermaritzbug in 1985 and 1986.

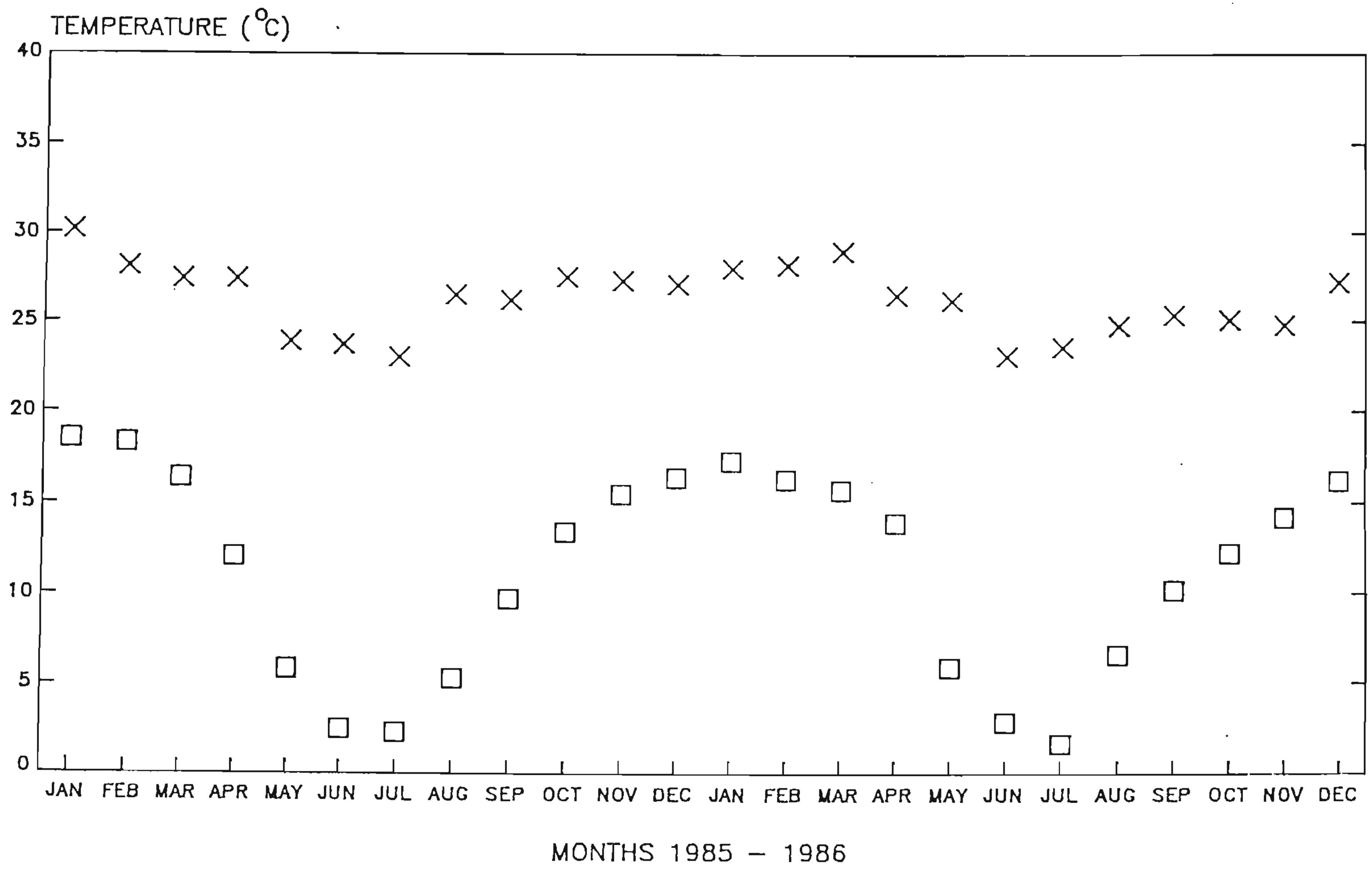


Fig. 4.6. Mean monthly maximum (x) and minimum (□) temperatures in Pietermaritzburg in 1985 and 1986.

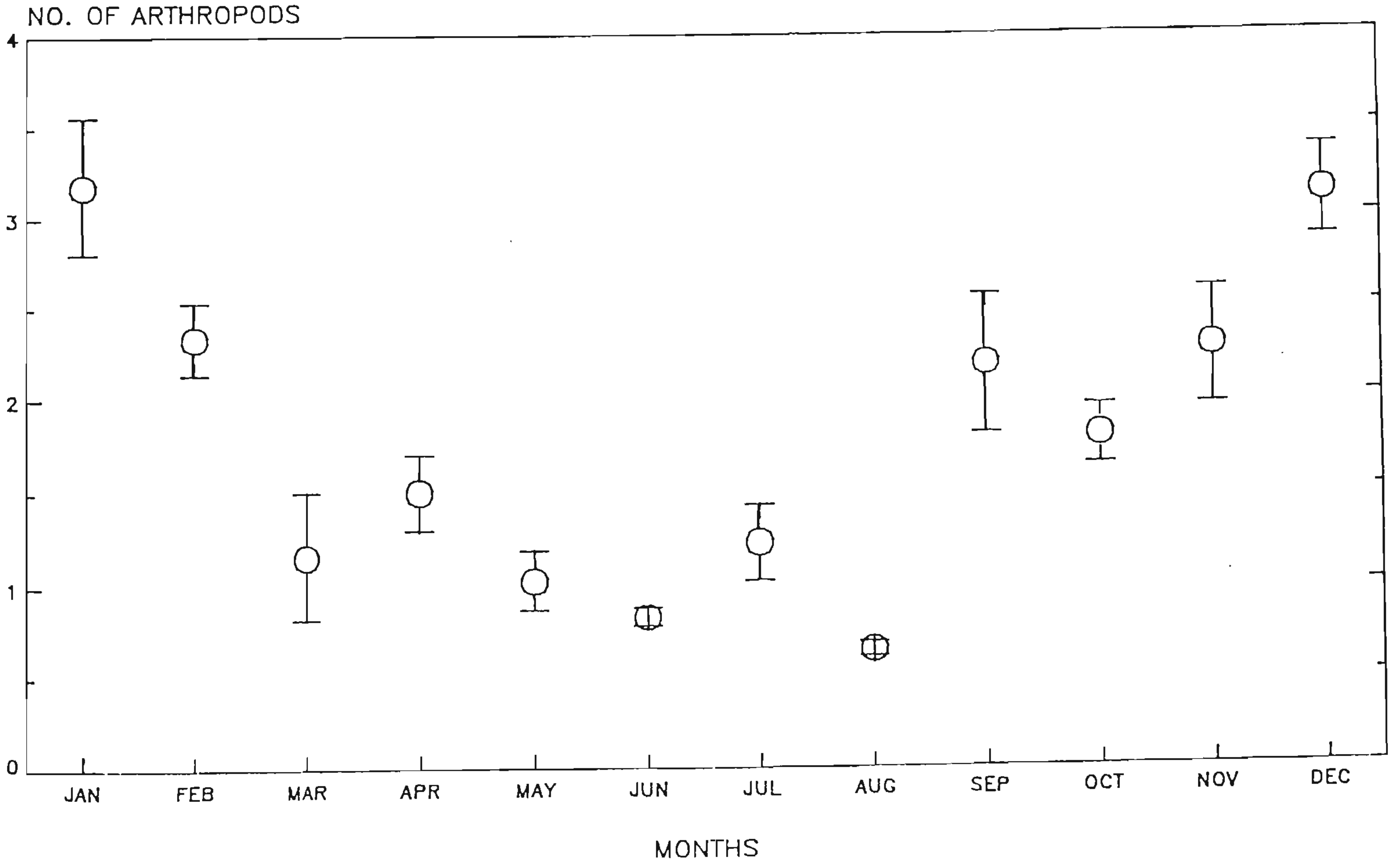


Fig. 4.7. Arthropod availability at Scottsville, Pietermaritzburg in 1986. Means (o) and standard errors (vertical lines) are plotted.

initiation and completion of egg-laying of Crowned, Blackwinged and Lesser Blackwinged Plovers in 1985 and 1986 are in Table 4.1.

In 1985, Crowned and Lesser Blackwinged Plovers in Ndumu started laying at the end of August and completed all clutches by the end of September. Summer rain was recorded from September 1985 (Chapter 5, Fig. 4). Minimum and maximum temperatures rose from July to September (Fig. 4.8) and were higher than the temperatures experienced in Pietermaritzburg in the corresponding months. In 1986, Crowned Plovers nested on Ndumu Estates in May and June (17 pairs) before any rain fell (Chapter 5, Fig. 4) and during two of the three coldest months of the year (Fig. 4.8). This unseasonal laying is ascribed to a flush of Harvester Termites <u>Hodotermes</u> <u>mossambicus</u> (see Chapter 5). In 1986, the first pair of Lesser Blackwinged Plovers to lay, completed their clutch on 3 September, while the last pair to lay in 1986 completed their clutch on 21 November. This protracted laying period can be ascribed to a lack of food (Fig. 4.9) since there was no rain in September 1986 (Chapter 5, Fig. 4), which also meant that the birds bred in the hottest months of the year (Fig. 4.8). In spring of 1986, Crowned Plovers started laying on 28 September and all had completed their clutches by 12 October 1986.

Mating system

One male Crowned Plover was found with two female Crowned

Table 4.1 Dates of initiation and completion of egg-laying of Crowned, Blackwinged and Lesser Blackwinged Plovers in 1985 and 1986.

Species	Year	Initiation	Completion
Crowned Plover			
Pietermaritzburg	1985	01 August	22 August
	1986	03 August	27 August
Ndumu	1985	23 August	13 September
	1986	28 September	12 October
Blackwinged Plover			
	1985	14 August	04 September
	1986	28 July	17 August
Lesser Blackwinged Plover			
	1985	26 August	24 September
	1986	03 September	21 November

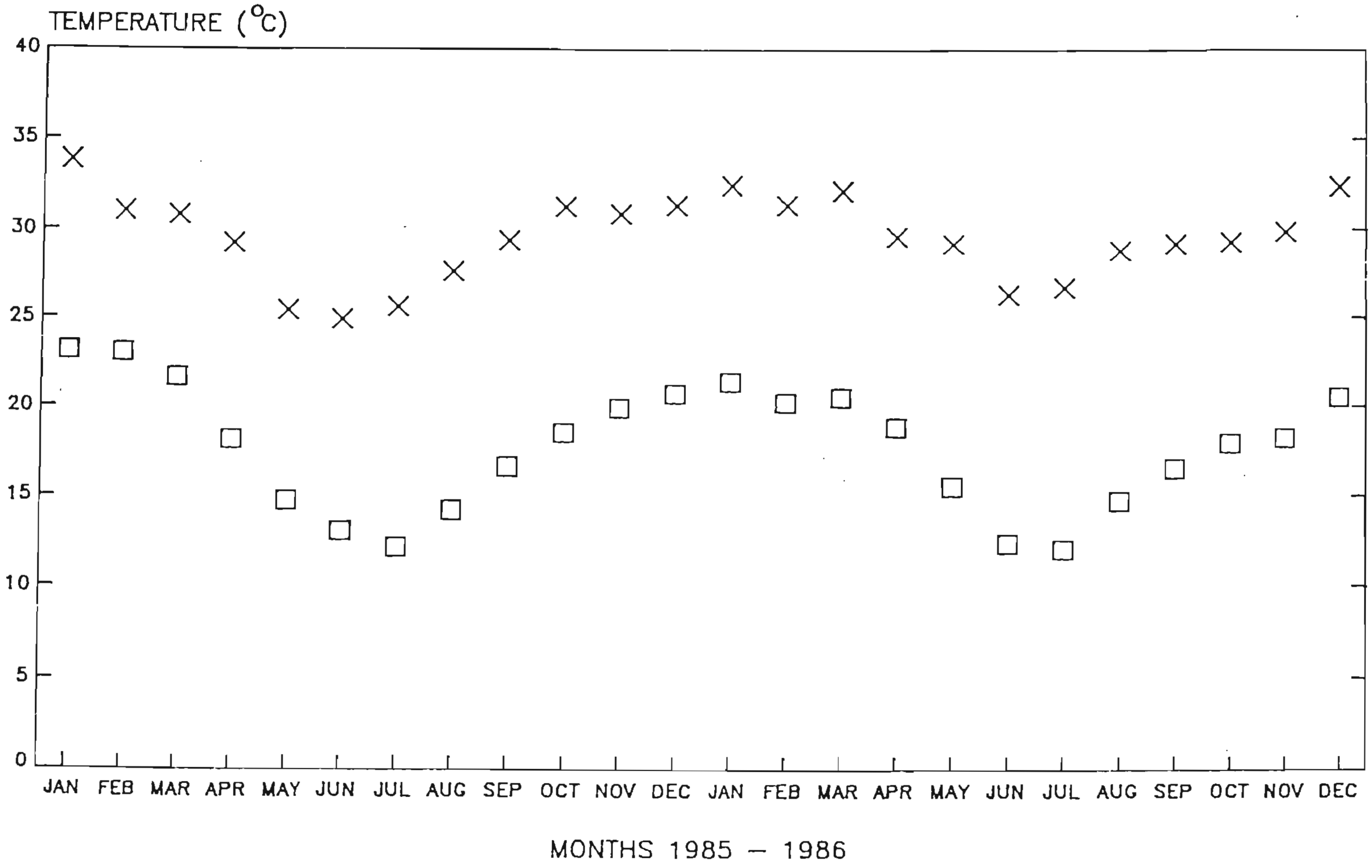


Fig.4.8. Mean monthly maximum (x) and minimum (□) temperatures at Ndumu in 1985 and 1986.

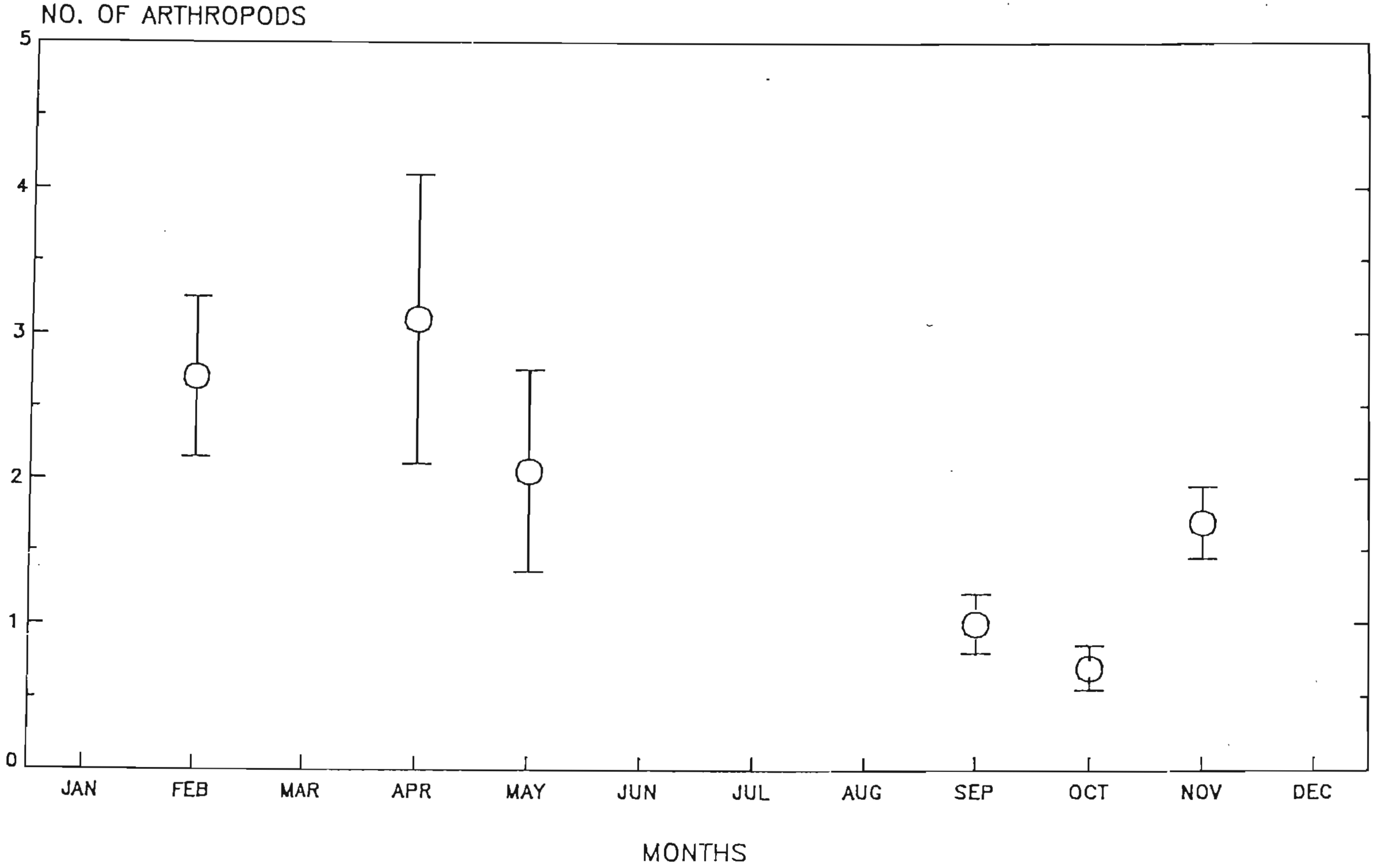


Fig. 4.9. Arthropod availability at Ndumu in 1986. Means (o) and standard errors (vertical lines) are plotted.

Plovers, each female having a nest. One nest had three eggs and the other one egg. The nests were 3 m apart. Only one nest was incubated and both were deserted three days after their discovery. All other Crowned Plovers, as well as all Blackwinged and Lesser Blackwinged Plovers in this study were monogamous.

Incubation

a) Crowned Plover

The incubation of seven Crowned Plover pairs was followed from the laying of the last egg of the clutch until the hatching of the last egg. One clutch was incubated for 29 days, another for 31 days and the rest for 30 days.

Crowned Plovers in Pietermaritzburg initiated incubation only after the clutch was completed, while Crowned Plovers in Ndumu started incubating after laying the first egg. Mean ±S.E. brood-patch temperatures of Crowned Plovers varied considerably with ambient temperature (Ndumu - x = 37,54 ±0,17 °C; Scottsville, Pietermaritzburg - x = 35,52 ±0,29 °C; combined Ndumu and Pietermaritzburg - x = 36,76 ±0,16 °C). Brood-patch temperatures were controlled at ambient temperatures above 30 °C (Fig. 4.10 and Fig. 4.11) and were not allowed to exceed 45,0 °C. Low ambient temperatures (below 13 °C) were not experienced during this study but it can be inferred from the slope of the regression line that this species also controls brood-patch

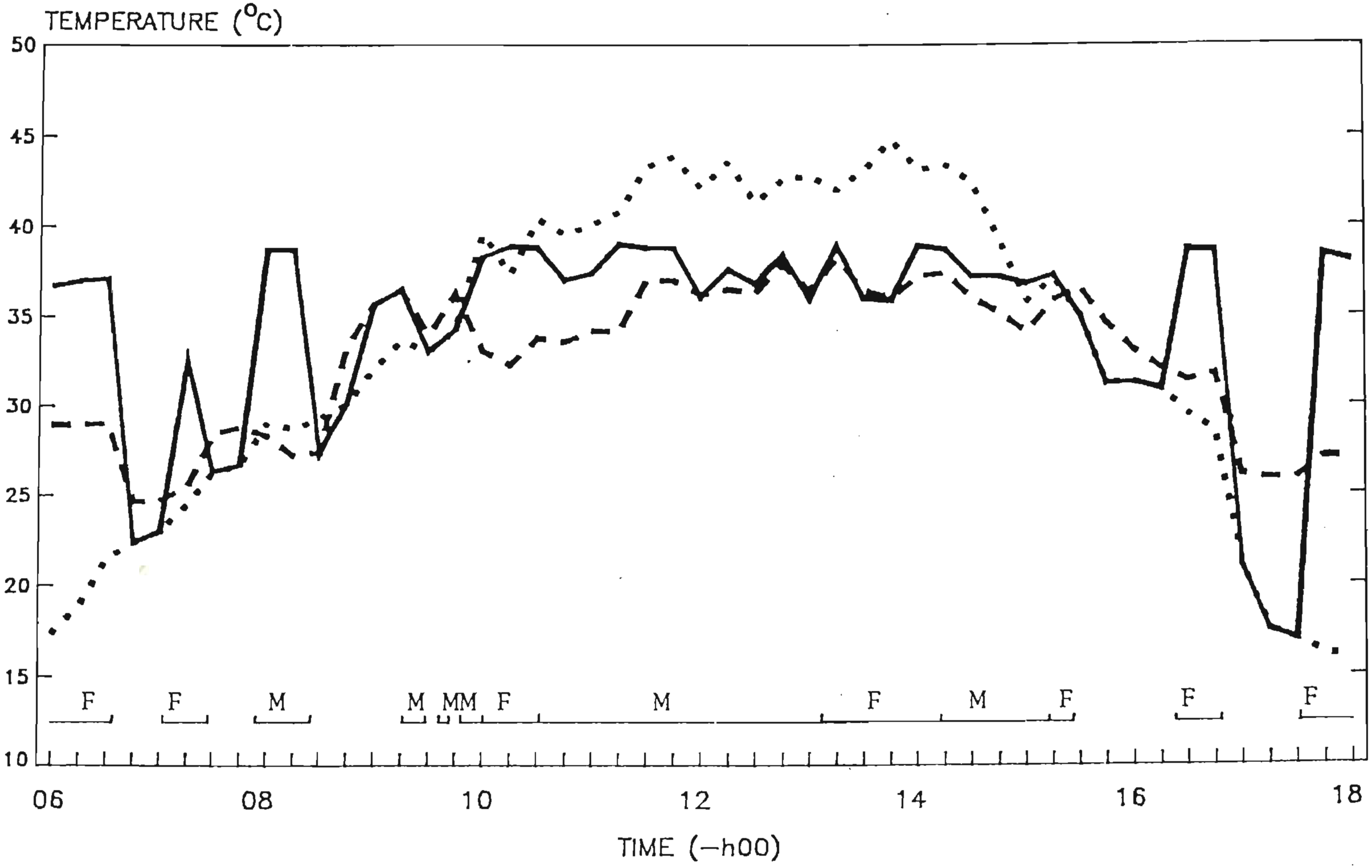


Fig. 4.10. A day of incubation of a Crowned Plover pair at Ndumu. M = male incubation bout, F = female incubation bout. Spaces indicate that the birds had vacated the nest. Solid line = brood-patch temperature; broken line = nest-air temperature; dotted line = ambient temperature.

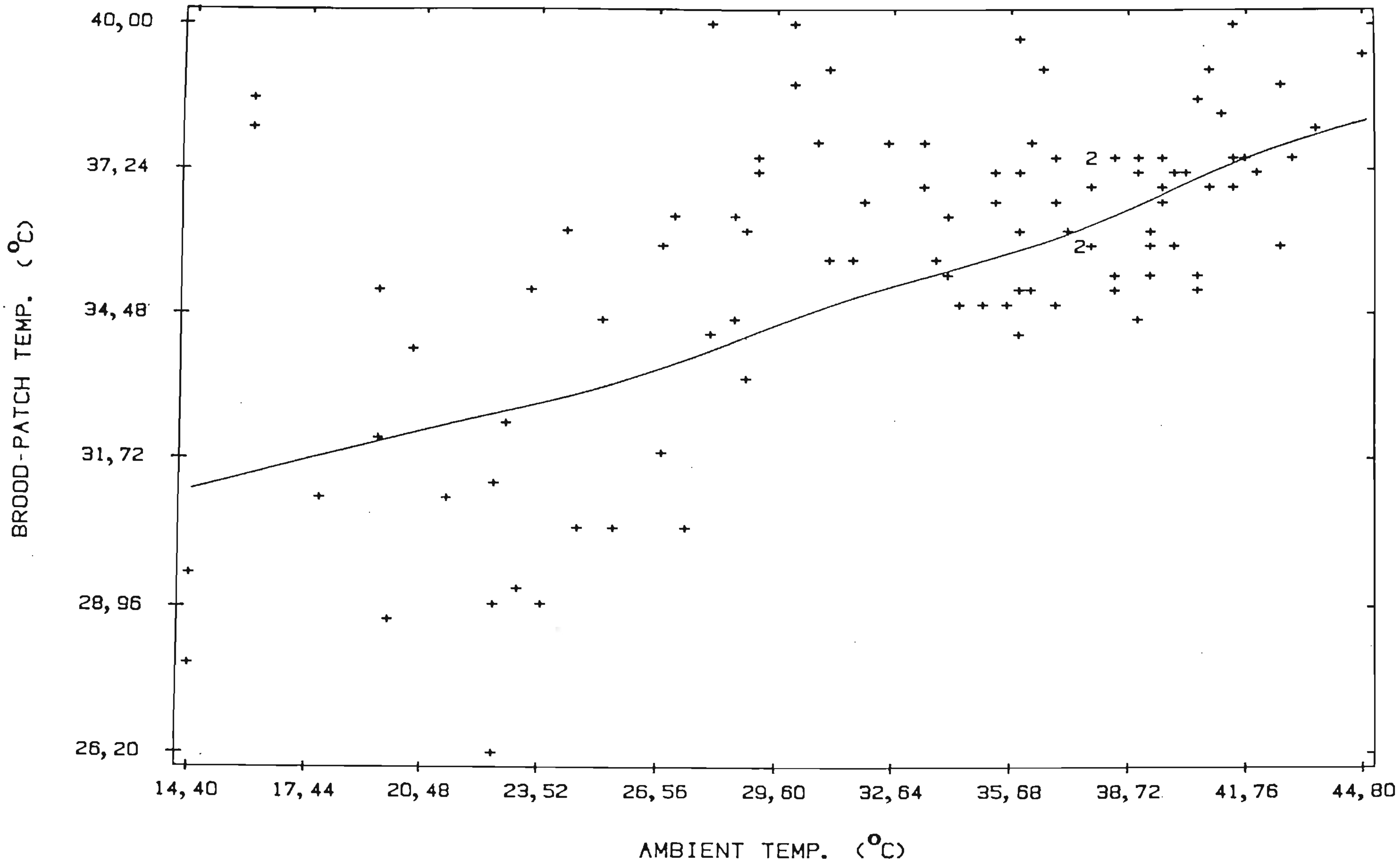


Fig. 4.11. Relationship between brood-patch temperature and ambient temperature in one Crowned Plover pair at Scottsville, Pietermaritzburg. Best-fit curve is $y = 1/(0,04 - 0,01x)$; $\underline{r}^2 = 0,39$; $p < 0,01$; $n = 101$. Numbers indicate the number of coinciding temperature values.

temperature at ambient temperatures below 17 °C, not allowing brood-patch temperatures to drop below 26,2 °C. The pair studied in Pietermaritzburg differed considerably in reaction to temperatures from those pairs studied in Ndumu (Fig. 4.12). The pair in Pietermaritzburg did not control brood-patch temperature at higher temperatures.

Mean ±S.E. nest-air temperatures of Crowned Plovers were 31,90 ±0,33 °C (Scottsville) (Fig. 4.13), 33,29 ±0,25 °C (Ndumu) (Fig. 4.14) and 32,74 +0,21 °C (combined) respectively. Nest-air temperatures of Crowned Plovers followed the same patterns as brood-patch temperature relative to ambient temperature (Fig. 4.15) except that at temperatures below 20 °C nest-air temperature dropped off sharply because of the drop in soil-surface temperatures, resulting in a change in the temperature gradient across the egg from 2 °C (ambient temperature = 50 °C) to 5 °C (ambient temperature = 13 °C).

Only female Crowned Plovers incubated at night and did most of the incubation during the day, although the percentage of incubation carried out by the male increased at higher ambient temperatures (Fig. 4.16).

Crowned Plovers orientated themselves with their backs to the sun while incubating at ambient temperatures above about 20 °C and faced the sun at ambient temperatures below this. When the sun was directly overhead and the wind blew harder than about 3 m/s

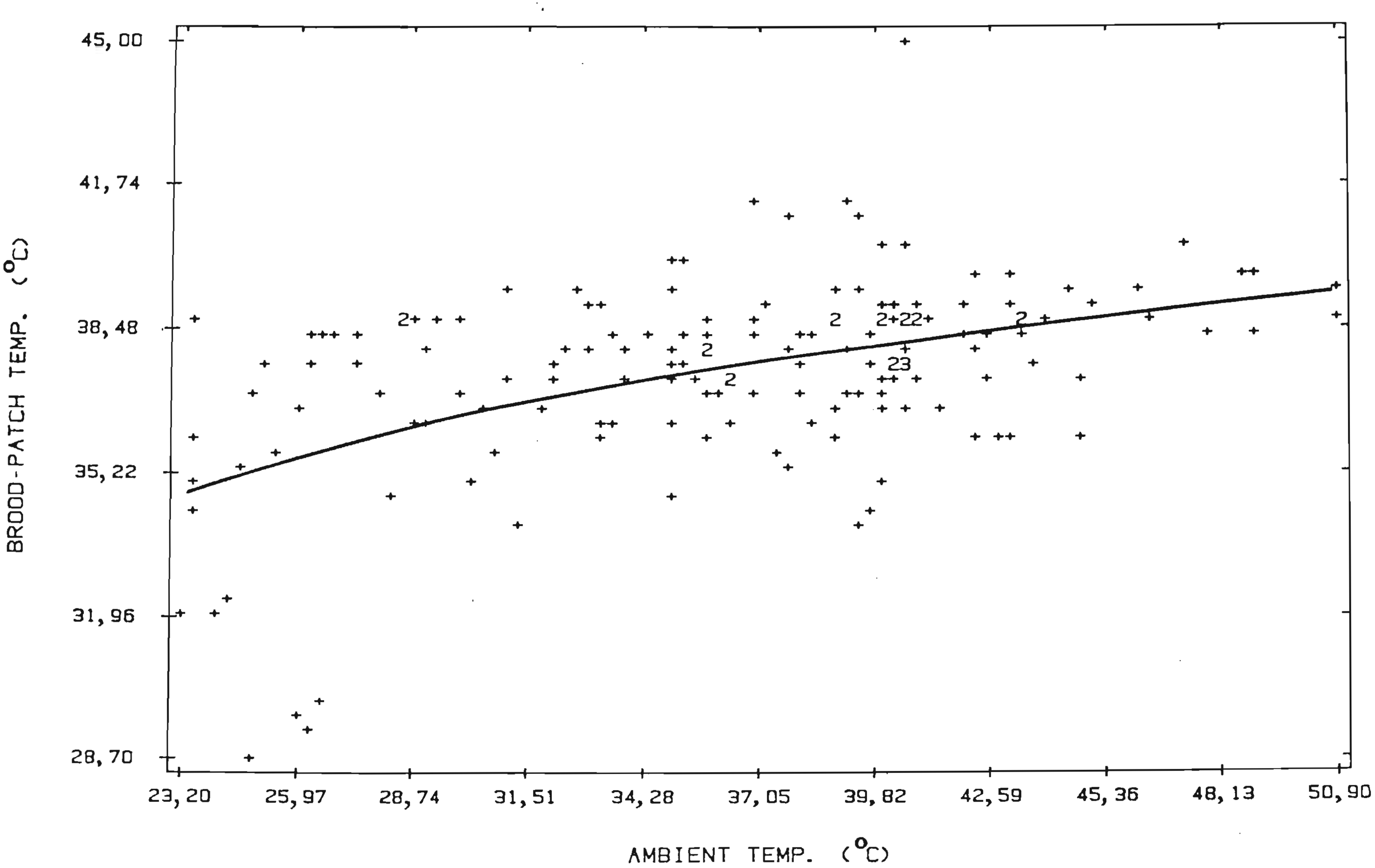


Fig. 4.12. Relationship between brood-patch temperature and ambient temperature in three Crowned Plover pairs at Ndumu. Best-fit curve is $y = e(3{,}77 - 5{,}23/x)$; $\underline{r}^2 = 0{,}25$; $p < 0{,}01$; $n = 161$. Numbers indicate the number of coinciding temperature values.

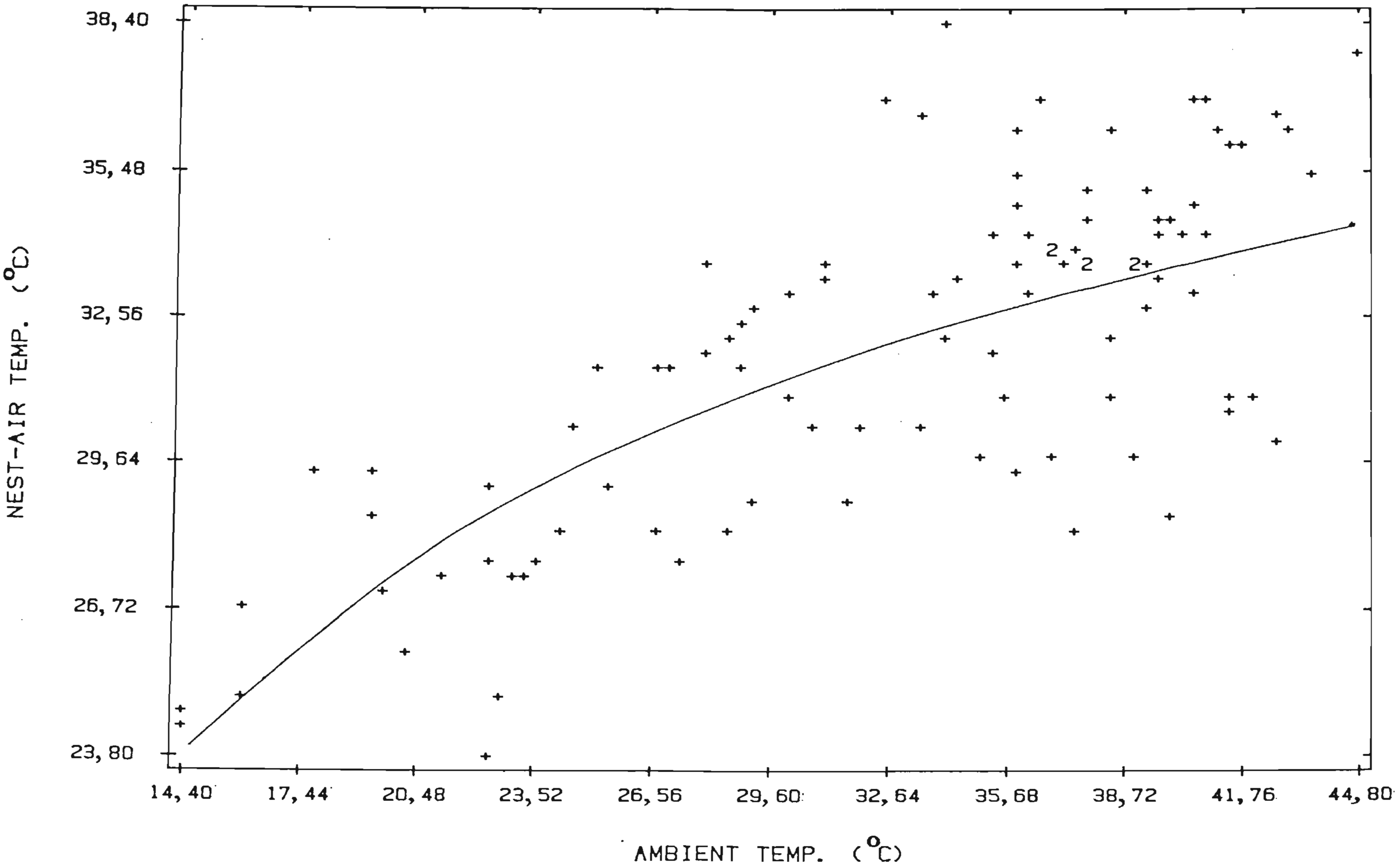


Fig. 4.13. Relationship between nest-air temperature and ambient temperature in a Crowned Plover pair at Scottsville, Pietermaritzburg. Best-fit curve is $y = x/(0,02x + 0,26)$; $\underline{r}^2 = 0,59$; $p < 0,01$; $n = 101$. Numbers indicate the number of coinciding temperature values.

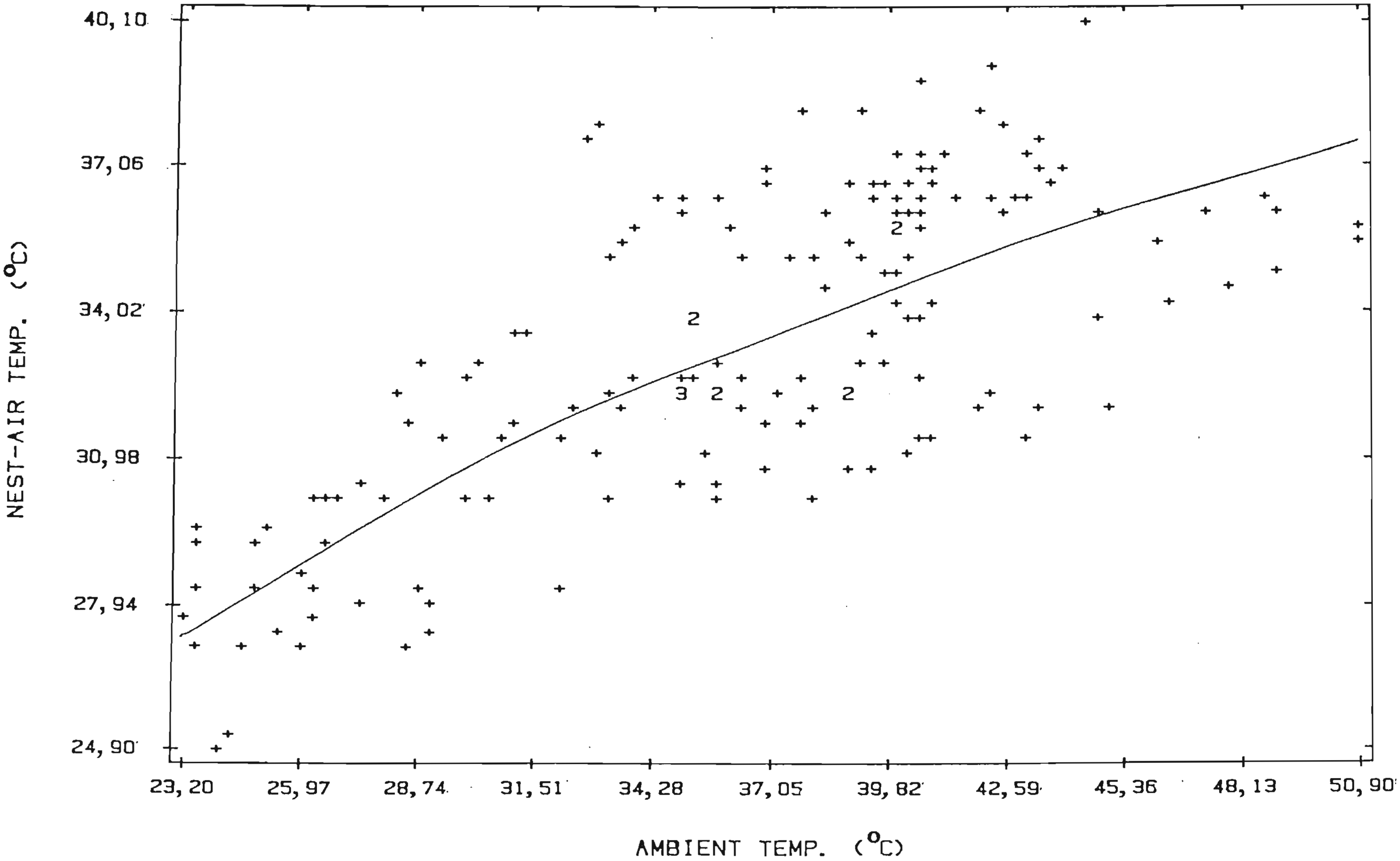


Fig. 4.14. Relationship between nest-air temperature and ambient temperature in three Crowned Plover pairs at Ndumu. Best-fit curve is $y = x/(0,02x + 0,42)$; $\underline{r}^2 = 0,61$; $p < 0,01$; $n = 161$. Numbers indicate the number of coinciding temperature values.

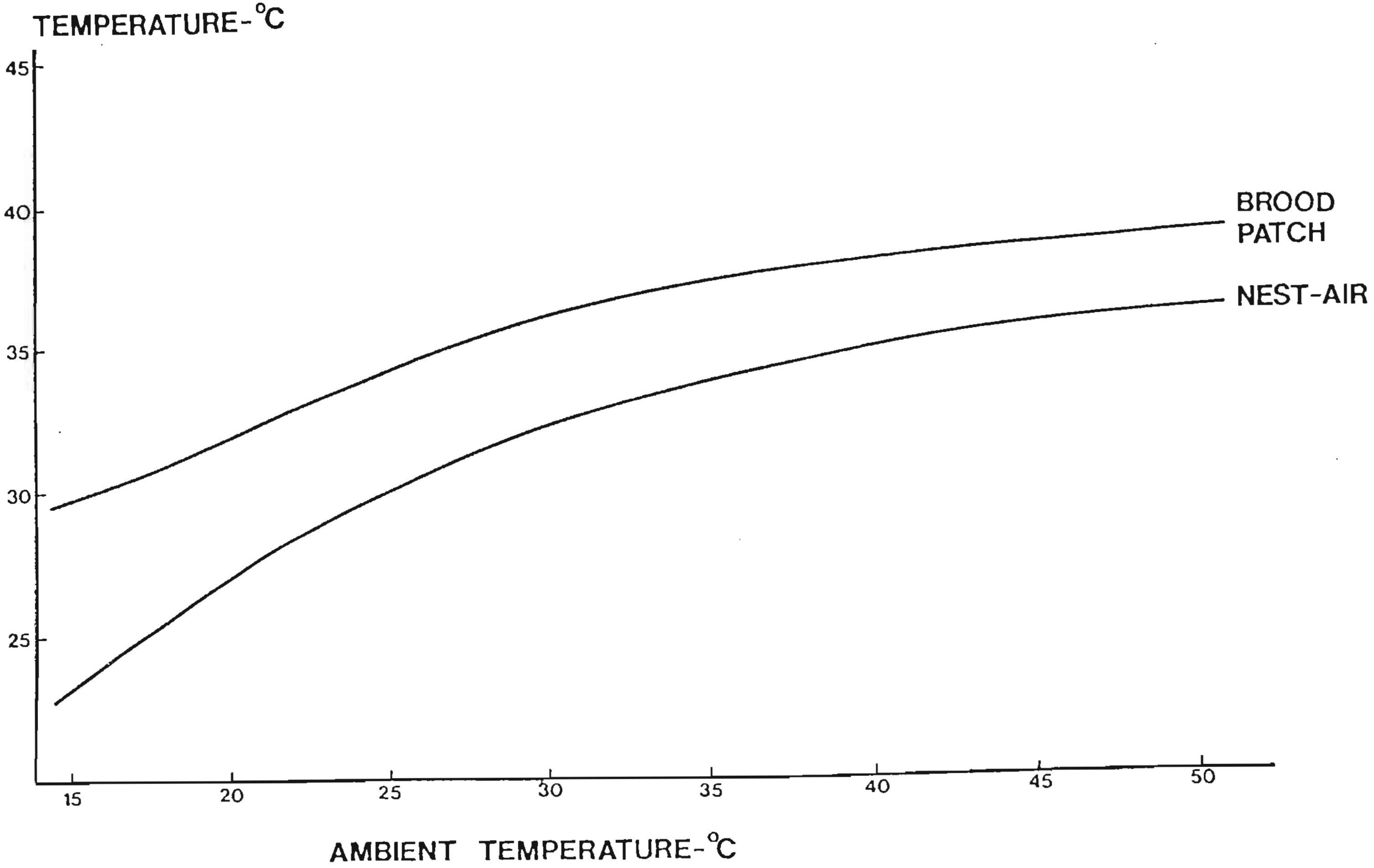


Fig. 4.15. Relationship between brood-patch and nest-air temperature and ambient temperature in 4 Crowned Plover pairs (combined data from Figs 4.11-4.14). Best-fit curve for brood-patch temperature against ambient temperature is $y = x/(0,02x + 0,16)$; $\underline{r}^2 = 0,36$; $p < 0,01$; $n = 262$. Best-fit curve for nest-air emperature against ambient temperature is $y = x/(0,02x + 0,32)$; $\underline{r}^2 = 0,59$; $p < 0,01$; $n = 262$.

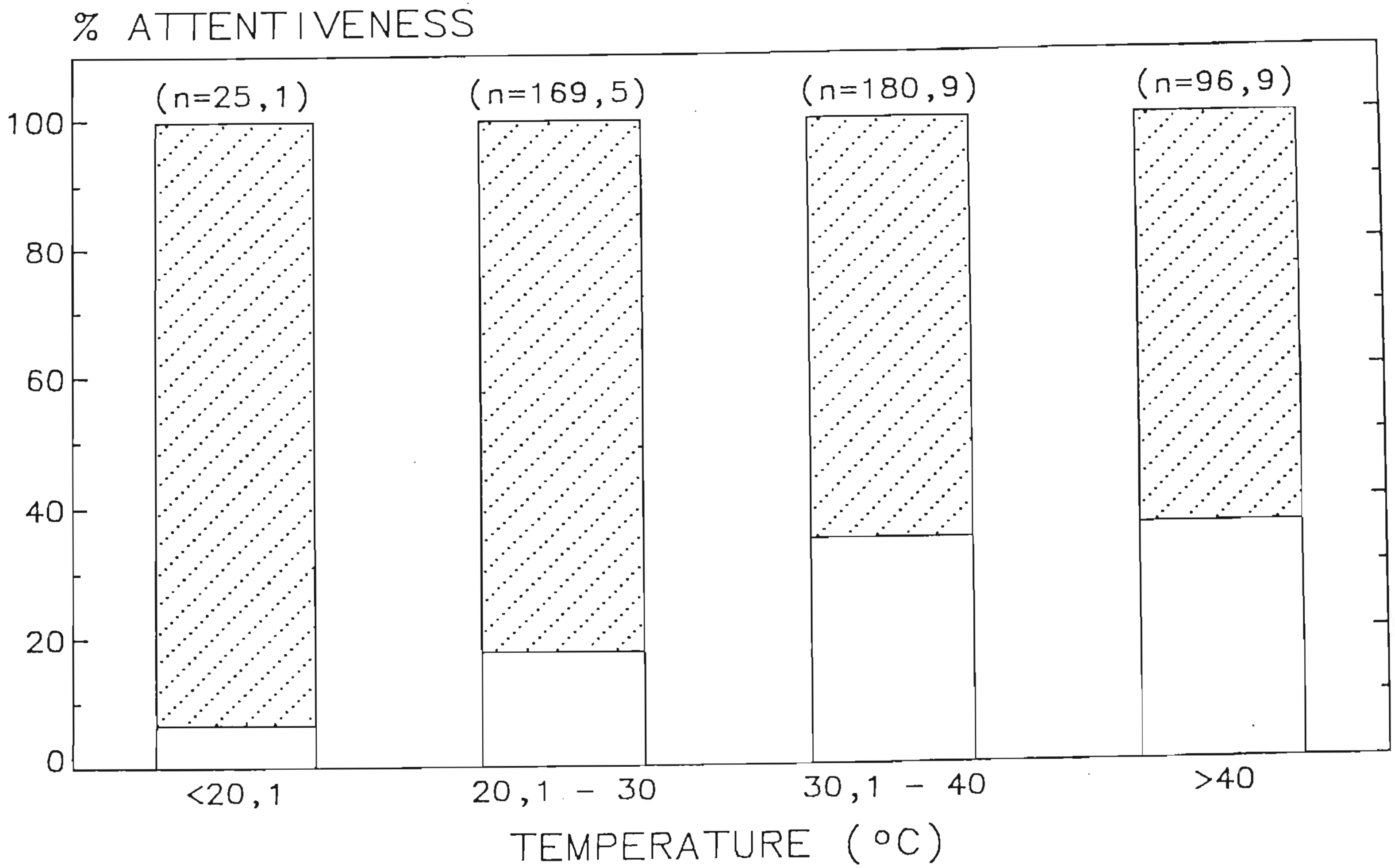


Fig. 4.16. Crowned Plover: nest attentiveness measured as a percentage of total time spent by male and female on the nest in each temperature category, for three pairs at Ndumu. n = number of hours of observation in each temperature category. Shaded area = female; unshaded = male.

then Crowned Plovers faced into the wind.

Nest attendance by both sexes increased at ambient temperatures below 20 ^{O}C and above 40 ^{O}C (Fig. 4.17), although total amount of time spent at the nest varied considerably (one pair at Scottsville spent 61,2% of the time off the nest - largely as a result of human disturbance - while the pairs at Ndumu Estates spent 22,2%, 18,2% and 18,5% off the nest. Both parents vacated the nest during morning and evening feeding periods. At higher ambient temperatures (above 35 ^{O}C) Crowned Plovers increased the amount of time spent shading the eggs (Fig. 4.18), although they did not shade if the wind speed was >3m/s. Shading behaviour involved squatting on the tibiotarsal joints with the body raised about 2 cm above the eggs. In addition, the birds raised the crown, neck and mantle feathers, the wings were drooped so that the wrist was below the level of the belly, the eyes swelled and took on a glazed appearance and, at temperatures above 47,7 ^{O}C, the birds fluttered the gular region. Panting behaviour in this species started at 39,8 ^{O}C while feather ruffling started at 37,2 ^{O}C. At high ambient temperatures (above about 35 ^{O}C), Crowned Plovers emitted a saline secretion (determined by taste) from their nostrils.

Nest-relief was controlled by the female, which frequently left the nest if the male did not respond to her krr-krr nest-relief call (not tape-recorded). The female relieved the male on the nest without the male making any vocalization to solicit nest

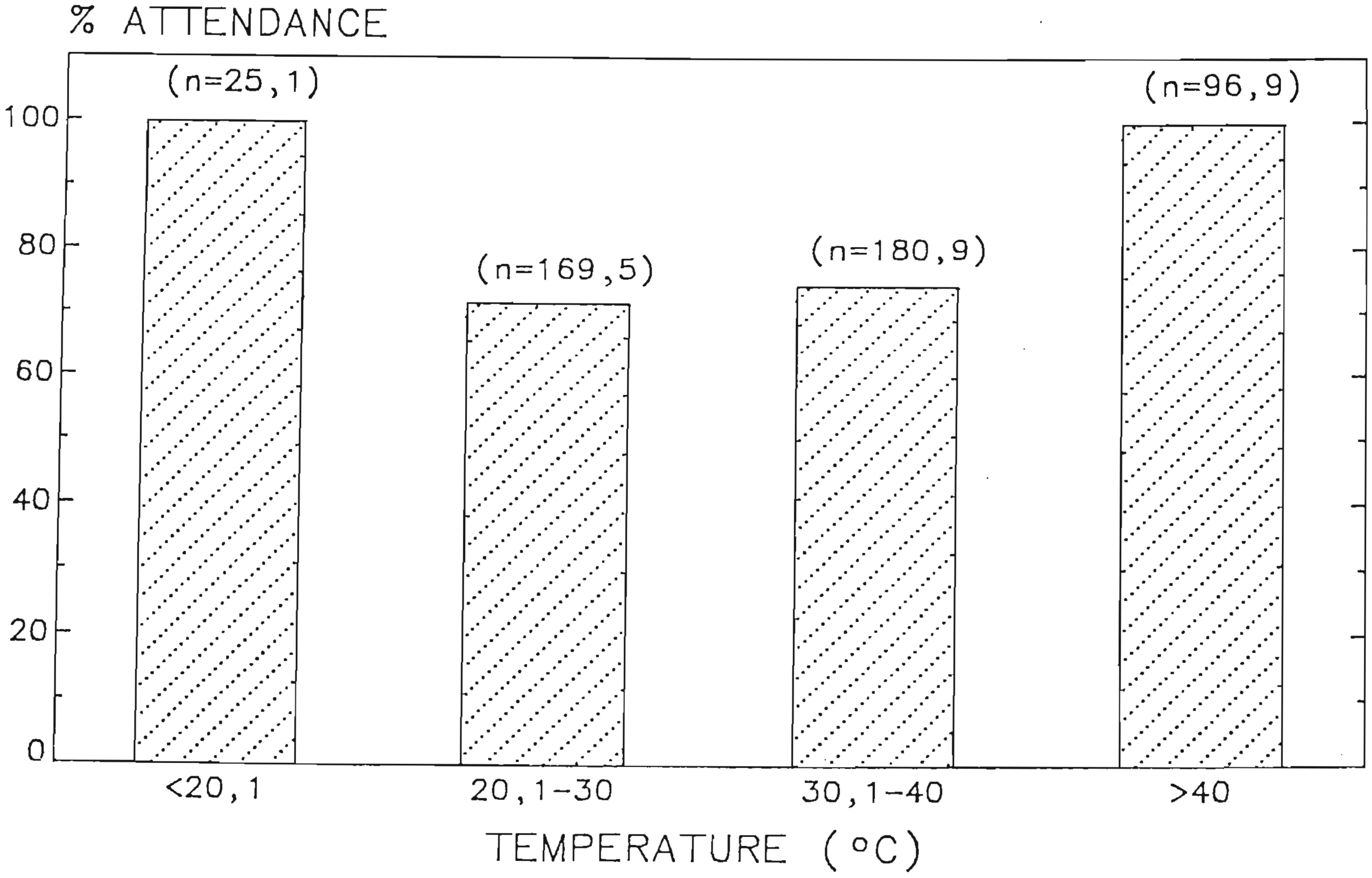


Fig. 4.17. Crowned Plover: nest attendance measured as a percentage of the total time spent observing three pairs at Ndumu. n = number of hours of observation in each temperature category.

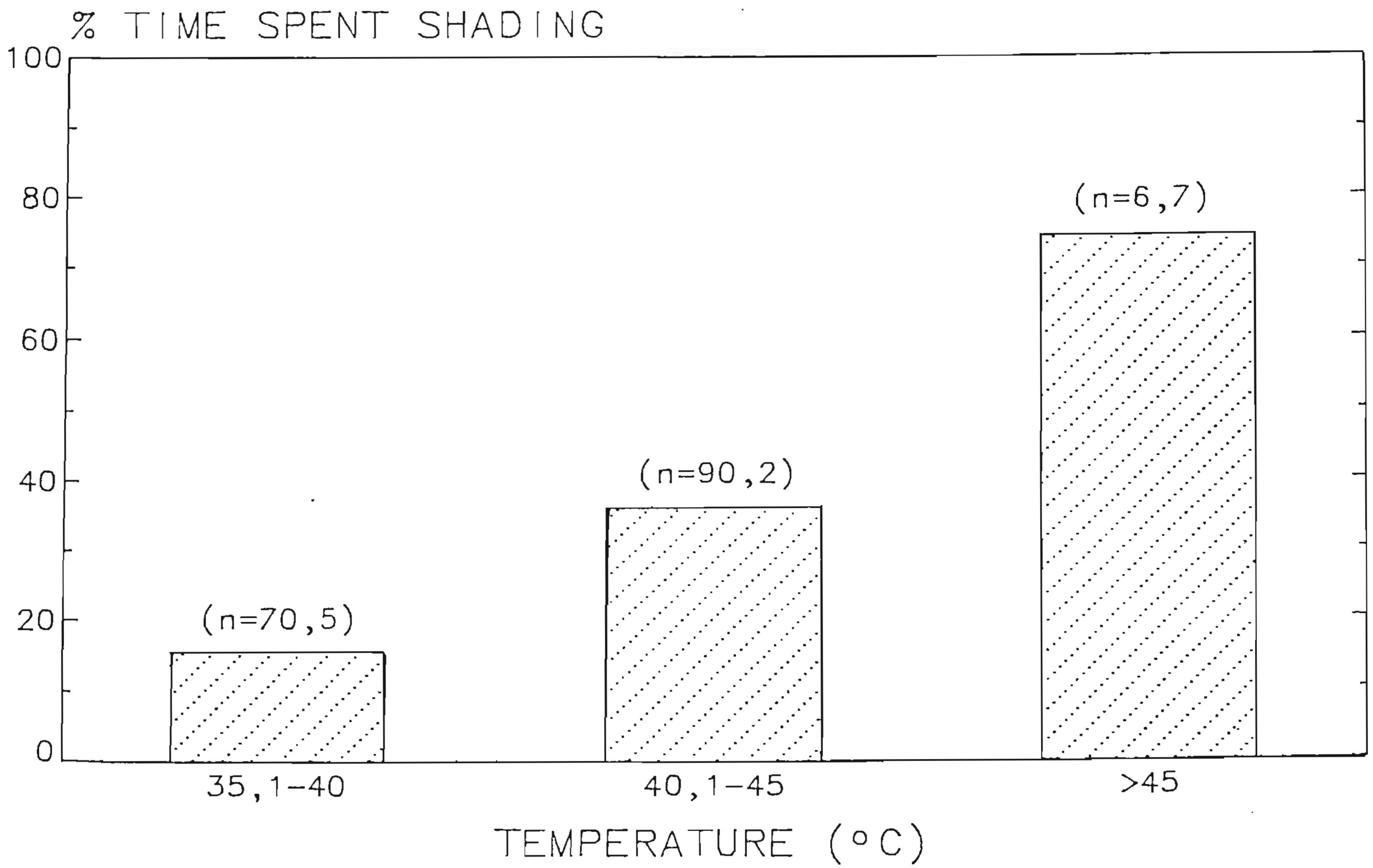


Fig. 4.18. Crowned Plover: time spent shading eggs measured as a percentage of total time spent observing three pairs at Ndumu. n = number of hours of observation in each temperature category.

relief. At nest-relief the sitting bird rose, picked up bits of dry or burnt grass, and tossed them about 5 cm into the nest, then walked about 1 m while continuing to sideways-throw. The sideways-throwing behaviour was frequently performed without the bird actually picking up an object. The relieved bird then walked away from the nest and stood in the shade if it was hot, or fed if the ambient temperature was moderate. When the sitting bird rose, the relieving bird walked to within 2 m of the nest and tossed grass sideways and then walked to the nest, shuffled grass around in the nest and rearranged the eggs before sitting on them.

The duration of incubation bouts varied considerably within each 10 °C ambient-temperature group (Fig. 4.19), with no significant difference between each group. Mean ±S.E. incubation-bout duration was 92,60 ±7,10 min.

b) Blackwinged Plover

The nests of six pairs of Blackwinged Plovers were watched from the laying of the last egg of the clutch until the hatching of the last egg. This period of incubation lasted 31 days in five clutches and 30 days in the other clutch.

Blackwinged Plovers initiated incubation only after the clutch was complete if ambient temperature rose above about 30 °C. Blackwinged Plovers maintain an almost constant brood-patch

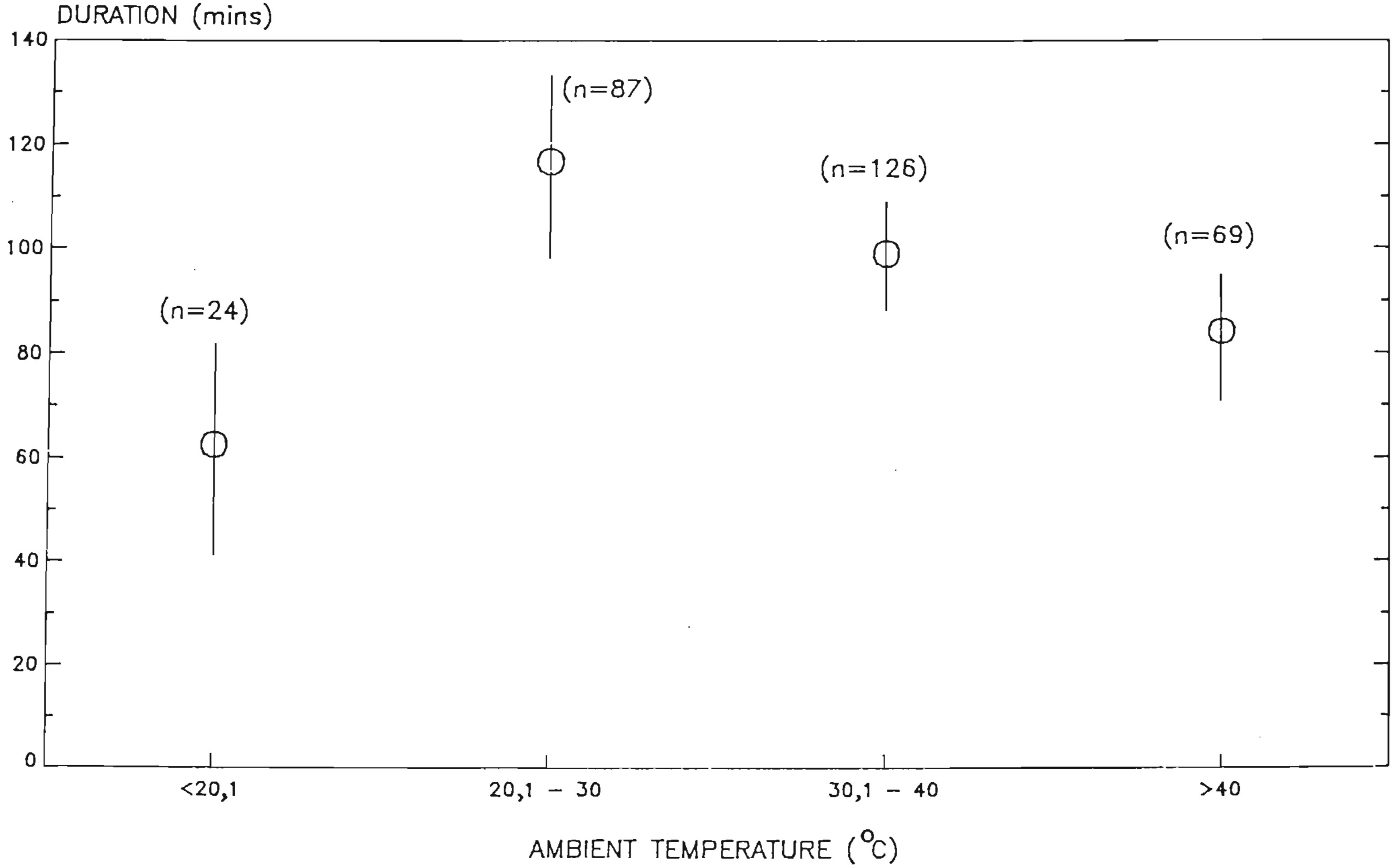


Fig. 4.19. Crowned Plover: incubation-bout duration in three pairs at Ndumu. Means (o) and 95% confidence limits (vertical lines) are plotted. n = number of incubation bouts observed in each temperature category.

temperature regardless of ambient temperature (Figs 4.20, 4.21 and 4.23). Nest-air temperatures increased logarithmically in the range of ambient temperatures measured (12,6-50,1 °C) (Figs 4.20 & 4.22), so that the temperature gradient across the egg was 15,1 °C at 12,6 °C as opposed to 1 °C at 50,1 °C (Fig. 4.23). Mean ±S.E. brood-patch and nest-air temperatures were 38,60 ±0,06 C and 30,83 ±0,27 °C, respectively.

Males incubated more at lower and higher temperatures and did more incubating than females at temperatures higher than 40 °C (Fig. 4.24). Females did all the incubating at night and controlled nest relief by day. Nest-relief behaviour followed exactly the same pattern described for Crowned Plovers. Nest attendance in both sexes was highest at higher temperatures (Fig. 4.25). Blackwinged Plovers left the nest unoccupied for 11,6% of the total time that nests were observed. Blackwinged Plovers did not vacate the nest to feed as did Crowned Plovers, but took turns to feed while the partner incubated.

Incubation-bout duration did not differ significantly over the temperature range measured (Fig. 4.26). Mean ±S.E. incubation-bout duration was 92,79 ±10,71 min. Shading behaviour was highest at temperatures above 45 °C (Fig. 4.27), although Blackwinged Plovers did not shade when the wind speed was >3 m/s. Blackwinged Plovers started ruffling their crown, neck and mantle feathers at ambient temperatures above 35,8 °C. Panting behaviour started at 36,6 °C, while gular fluttering was initiated at 40,8 °C.

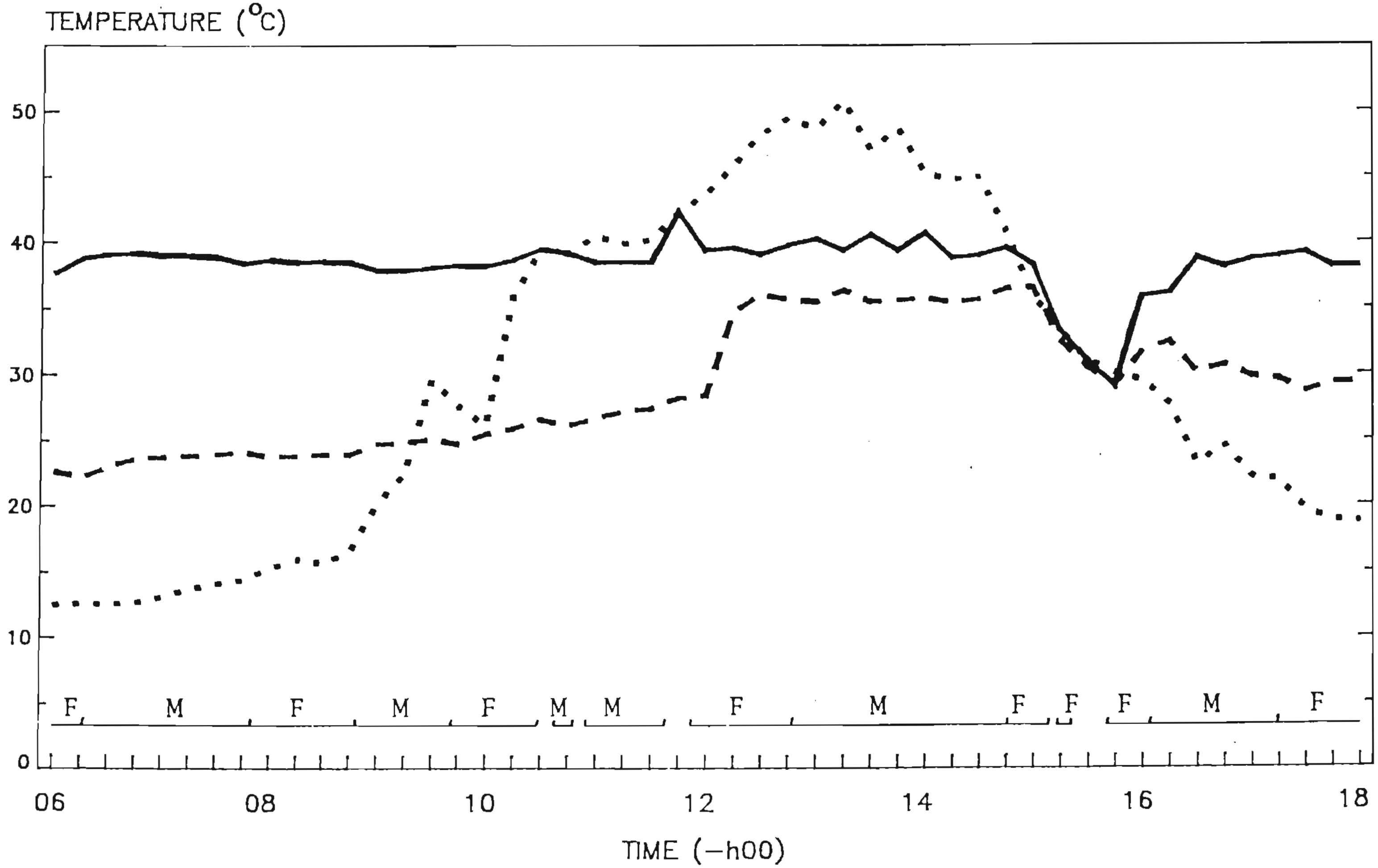


Fig. 4.20. A day of incubation of a Blackwinged Plover pair at Pietermaritzburg. M = male incubation bout, F = female incubation bout. Spaces indicate that the birds had vacated the nest. Solid line = brood-patch temperature; broken line = nest-air temperature; dotted line = ambient temperature.

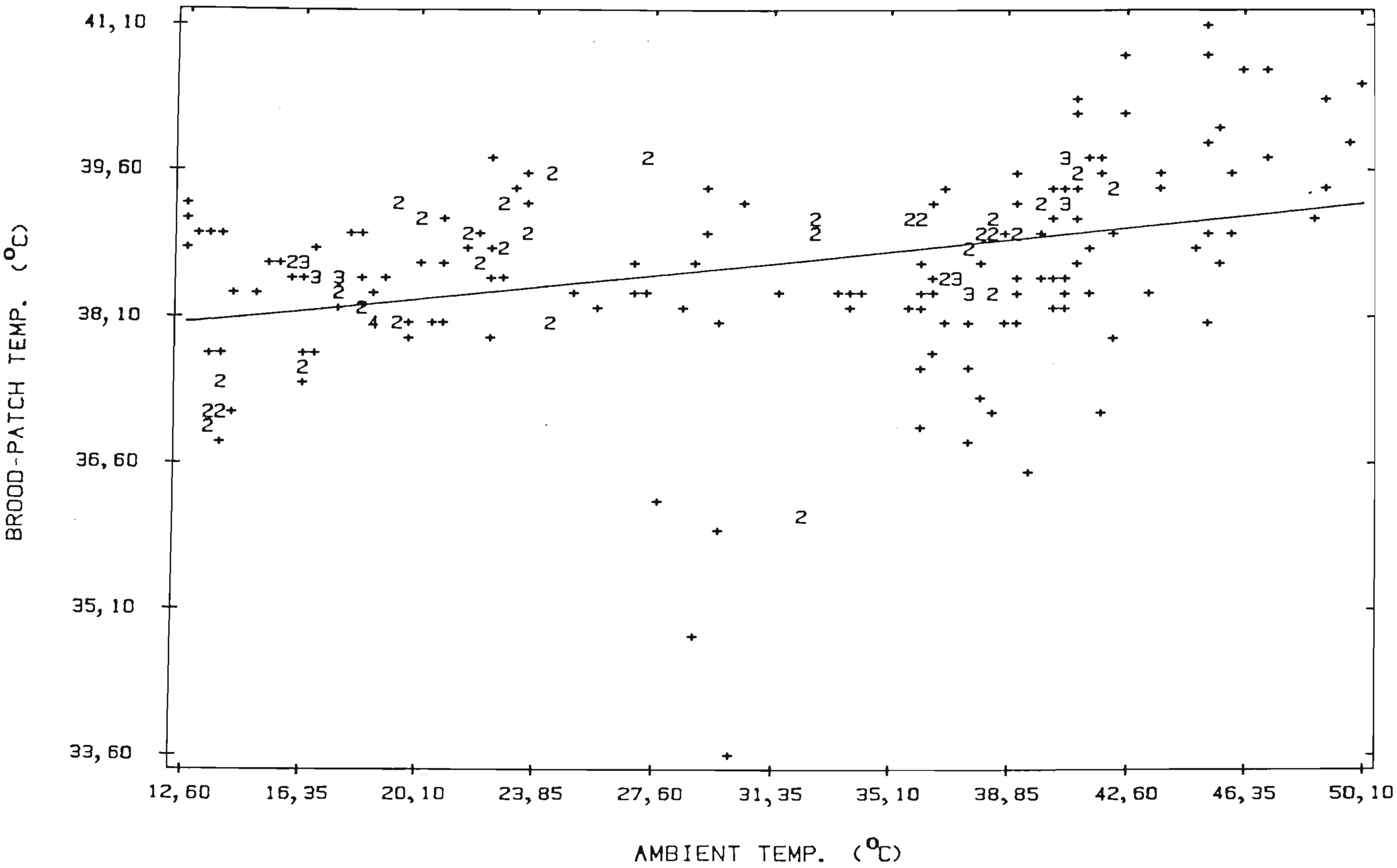


Fig. 4.21. Relationship between brood-patch temperature and ambient temperature in three Blackwinged Plover pairs at Pietermaritzburg. Best-fit curve is $y = 37,68 + 0,03x$; $\underline{r}^2 = 0,12$; $p < 0,01$; $n = 226$. Numbers indicate the number of coinciding temperature values.

However, of all the mixed-species colonies seen, only in the association of Redwinged Pratincoles and Crowned Plovers is there a feeding separation because Redwinged Pratincoles are aerial feeders, although their chicks are not. All of the mixed-species nesting associations which included Crowned Plovers were advantageous to those species nesting with them because they are aggressive mobbers of predators. This association is potentially disadvantageous to Crowned Plovers because of interspecific competition for food, although this never occurred because Crowned Plovers took the feeding territories they required and the other species nested near them. The association between Lesser Blackwinged Plovers and Redeyed Doves was more unusual because of the different nesting requirements. However, this association has no disadvantages and has the advantage of the dove being better able to warn the plover of the presence of an avian predator while the plover warned and distracted terrestrial predators such as Slender Mongoose _Galerella_ _sanguinea_ which unsuccessfully attacked both species on two occasions.

"Rapes" observed in Crowned Plovers (also called kleptogamy (Hamilton 1971)) followed the "hawk-dove strategy" predicted by Maynard-Smith (1982) because the intruder ("dove"), who stood to gain by spreading his genes, is submissive once confronted by the territory owner ("hawk") since he would gain nothing from winning a fight with the "hawk" and taking over the female because the "hawk" would no longer look after the "dove's" genes. Kleptogamy is both an advantage and a disadvantage of colonial life; because

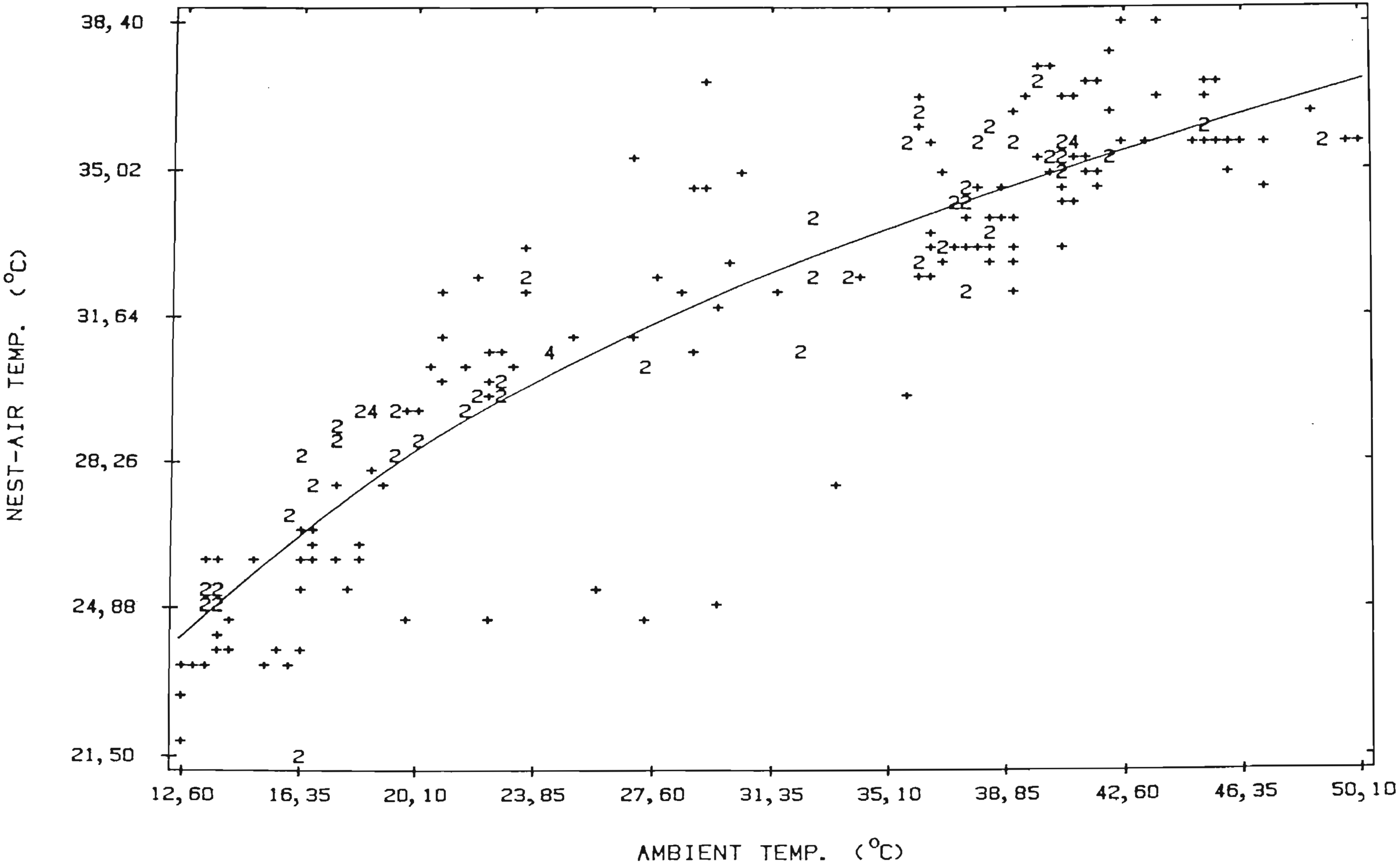


Fig. 4.22. Relationship between nest-air temperature and ambient temperature in three Blackwinged Plover pairs at Pietermaritzburg. Best-fit curve is $y = 0{,}40 + 9{,}36x$; $\underline{r}^2 = 0{,}83$; $p < 0{,}01$; $n = 226$. Numbers indicate the number of coinciding temperature values.

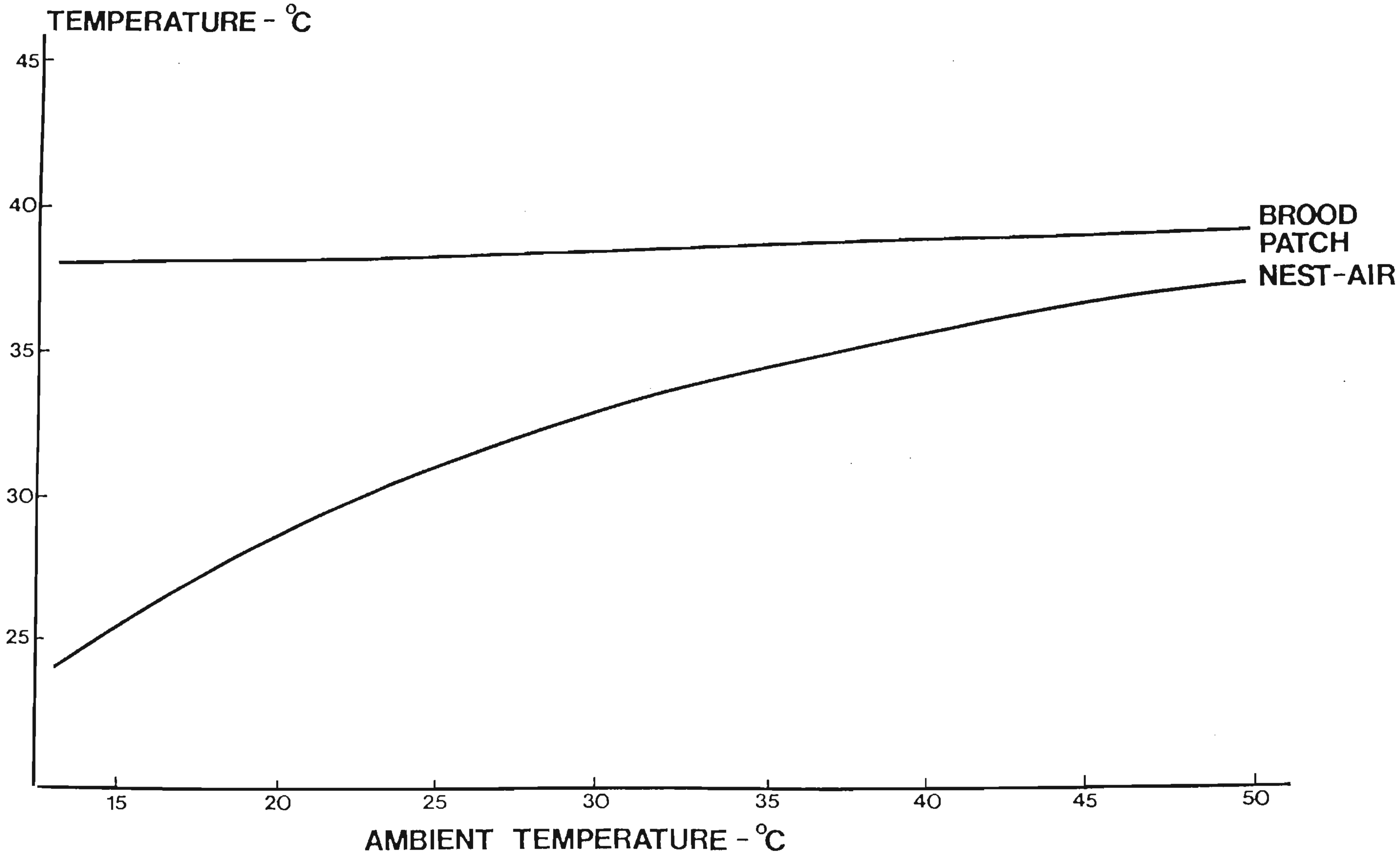


Fig. 4.23. Relationship between brood-patch and nest-air temperature and ambient temperature in three Blackwinged Plover pairs at Pietermaritzburg to demonstrate the gradient over the egg caused by the difference between brood-patch and nest-air temperature. Best-fit curves as for Figs 4.21 and 4.22.

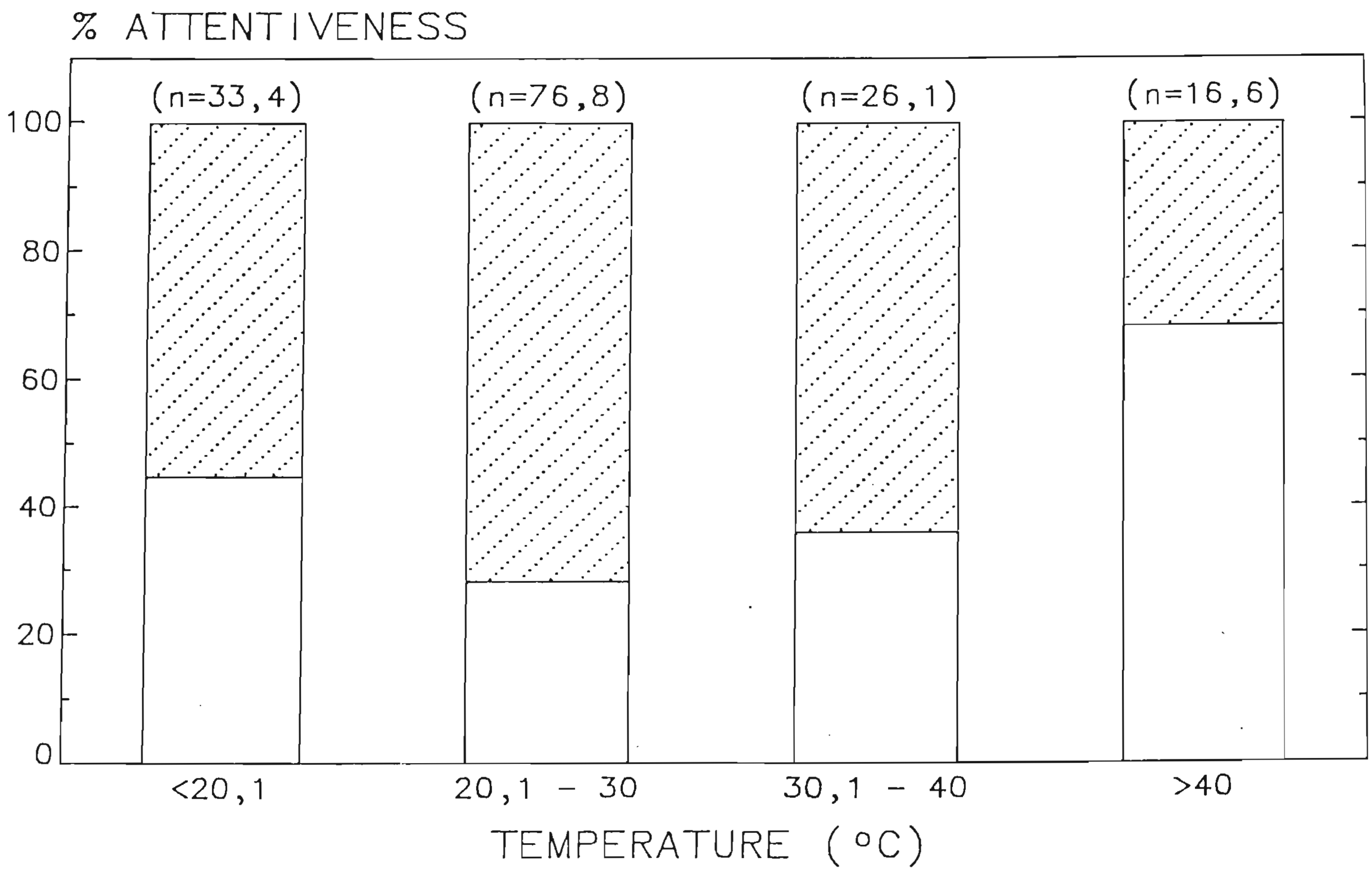


Fig. 4.24. Blackwinged Plover: nest attentiveness measured as a percentage of total time spent by male and female on the nest in each temperature category, for three pairs at Pietermaritzburg. n = number of hours of observation in each temperature category. Shaded area = female; unshaded = male.

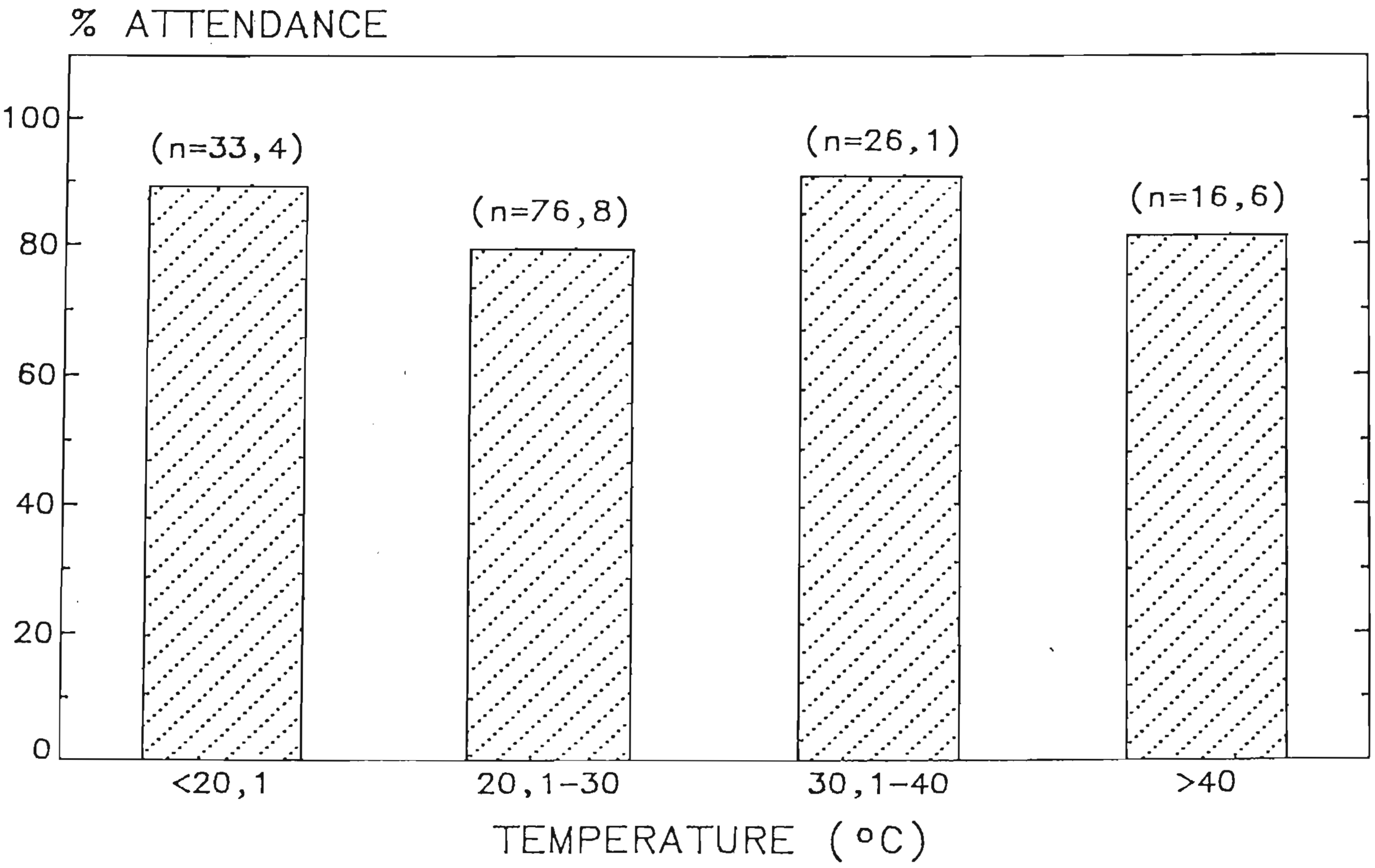


Fig. 4.25. Blackwinged Plover: nest attendance measured as a percentage of the total time spent observing three pairs at Pietermaritzburg. n = number of hours of observation in each temperature category.

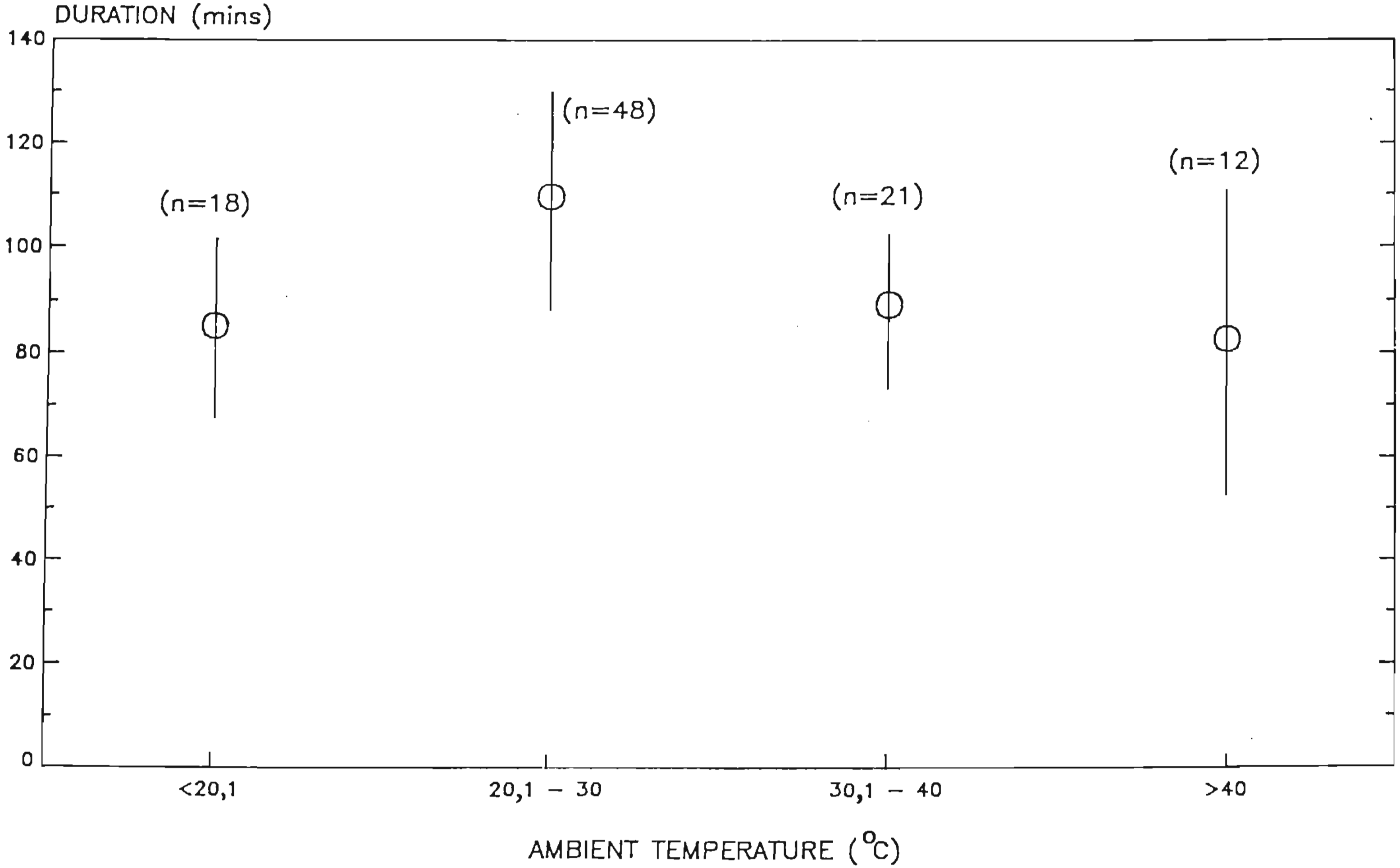


Fig. 4.26. Blackwinged Plover: incubation bout duration in three pairs at Pietermaritzburg. Means (o) and 95% confidence limits (vertical lines) are plotted. n = number of incubation bouts observed in each temperature category.

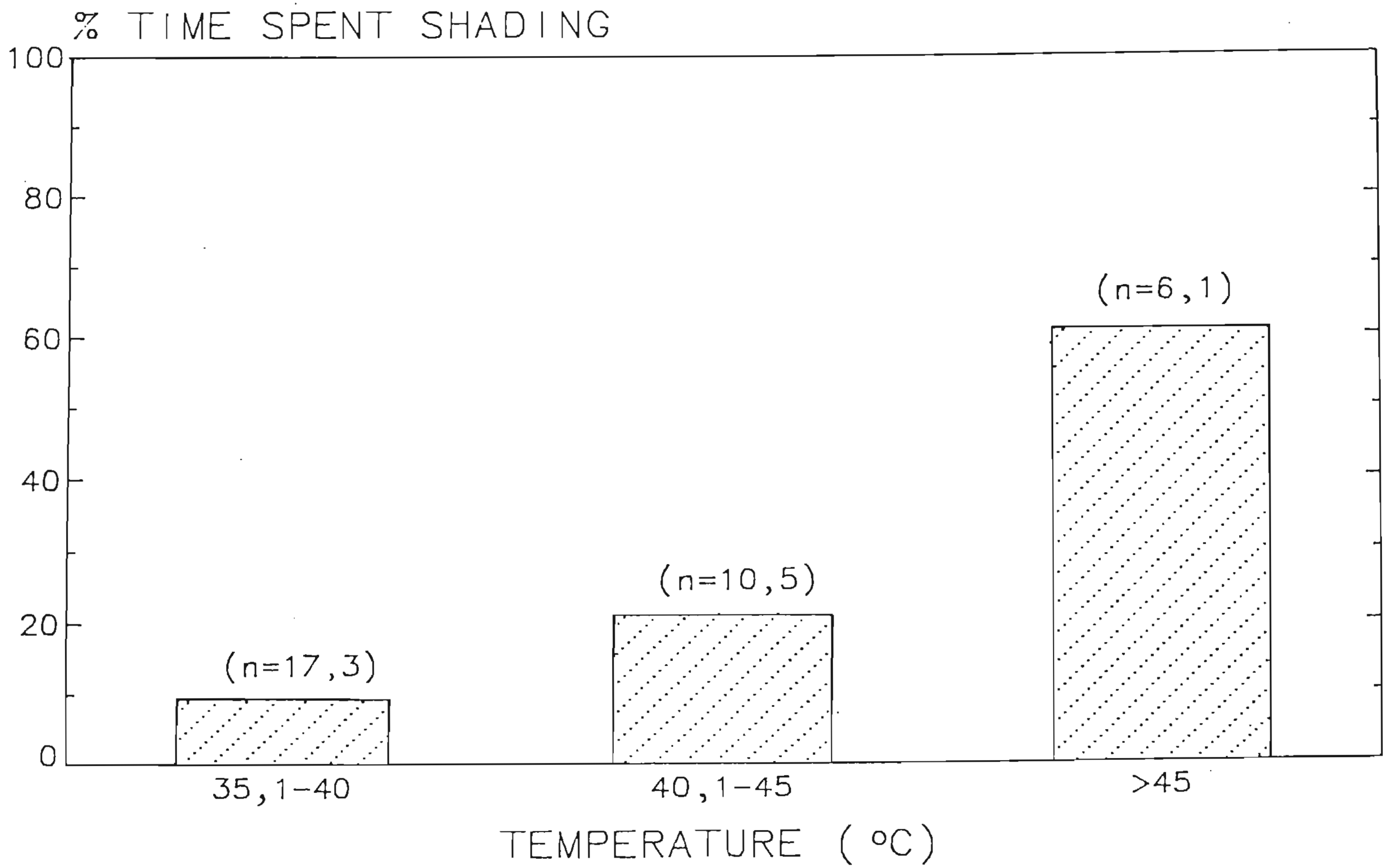


Fig. 4.27. Blackwinged Plover: time spent shading eggs measured as a percentage of total time spent observing three pairs at Pietermaritzburg. n = number of hours of observation in each temperature category.

A saline secretion was exuded from the nostrils (determined by taste) at temperatures above about 35 °C. These birds appeared to suffer from heat stress at ambient temperatures above 44,5 °C, when they started uttering <u>tiow-tiow</u> calls (not tape-recorded) and shuffling about intermittently on the nest. Blackwinged Plovers followed the same orientation patterns as Crowned Plovers with respect to sun and wind.

c) <u>Lesser Blackwinged Plover</u>

The nests of four pairs of Lesser Blackwinged Plovers were watched from the laying of the last egg of the clutch until the last egg hatched. Three clutches took 27 days to hatch while one took 28 days.

Lesser Blackwinged Plovers initiated incubation immediately after laying the first egg. Brood-patch temperatures increased with increasing ambient temperatures in the range of ambient temperatures measured (17,0-50,6 °C) with a mean ±S.E. value of 37,78 ±0,27 °C (Figs 4.28 & 4.29). Nest-air temperatures also increased with increasing ambient temperatures (Fig. 4.28 and 4.30) with a mean ±S.E. nest-air temperature of 34,11 ±0,25 °C being recorded. The gradient in temperature across the egg remained constant at 3,7 °C (Fig. 4.31).

Males did no incubating at ambient temperatures below 20 °C. They increased the percentage of time spent incubating in each 10 °C

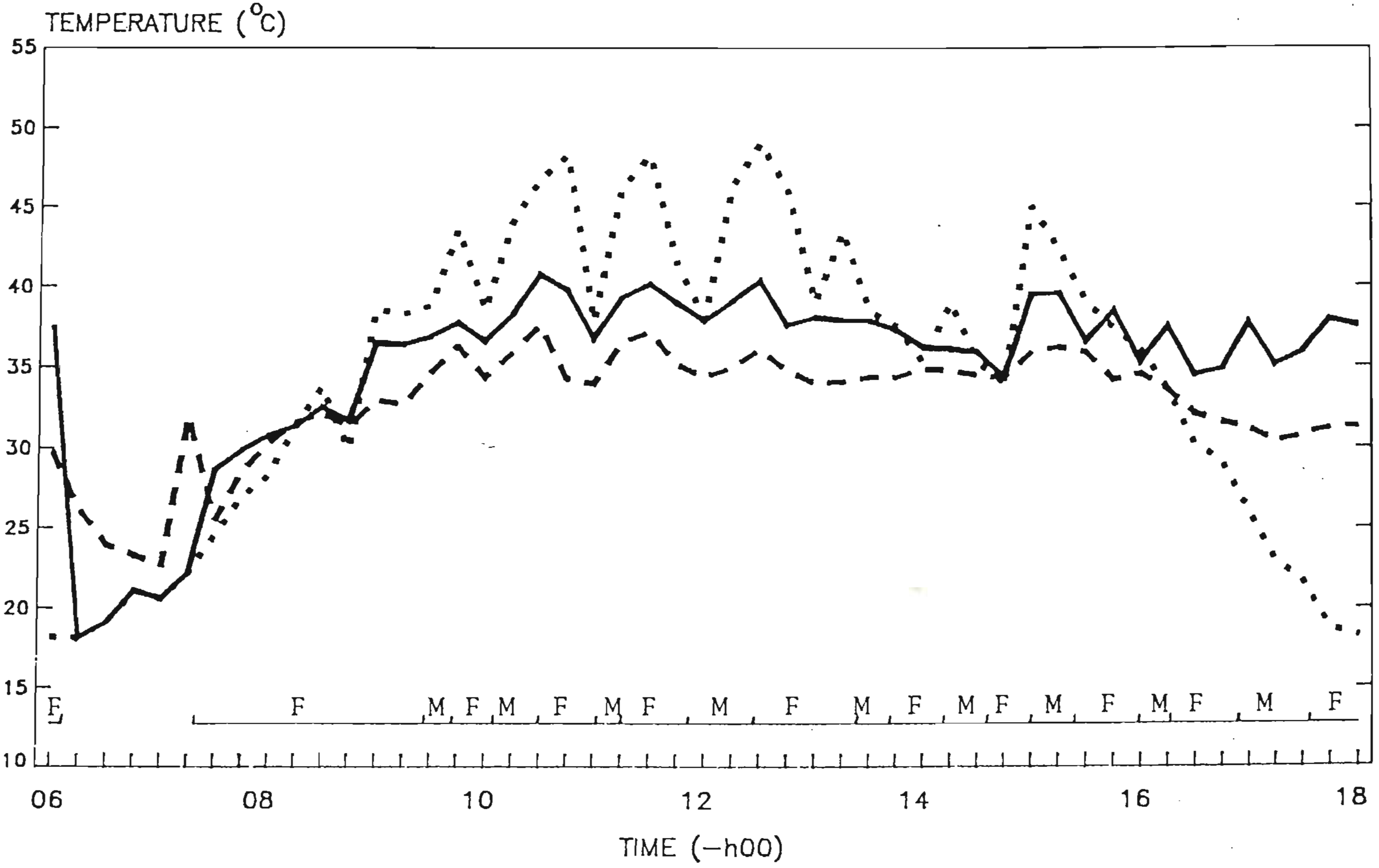


Fig. 4.28. A day of incubation of a Lesser Blackwinged Plover pair at Ndumu. M = male incubation bout, F = female incubation bout. Spaces indicate that the birds had vacated the nest. Solid line = brood-patch temperature; broken line = nest-air temperature; dotted line = ambient temperature.

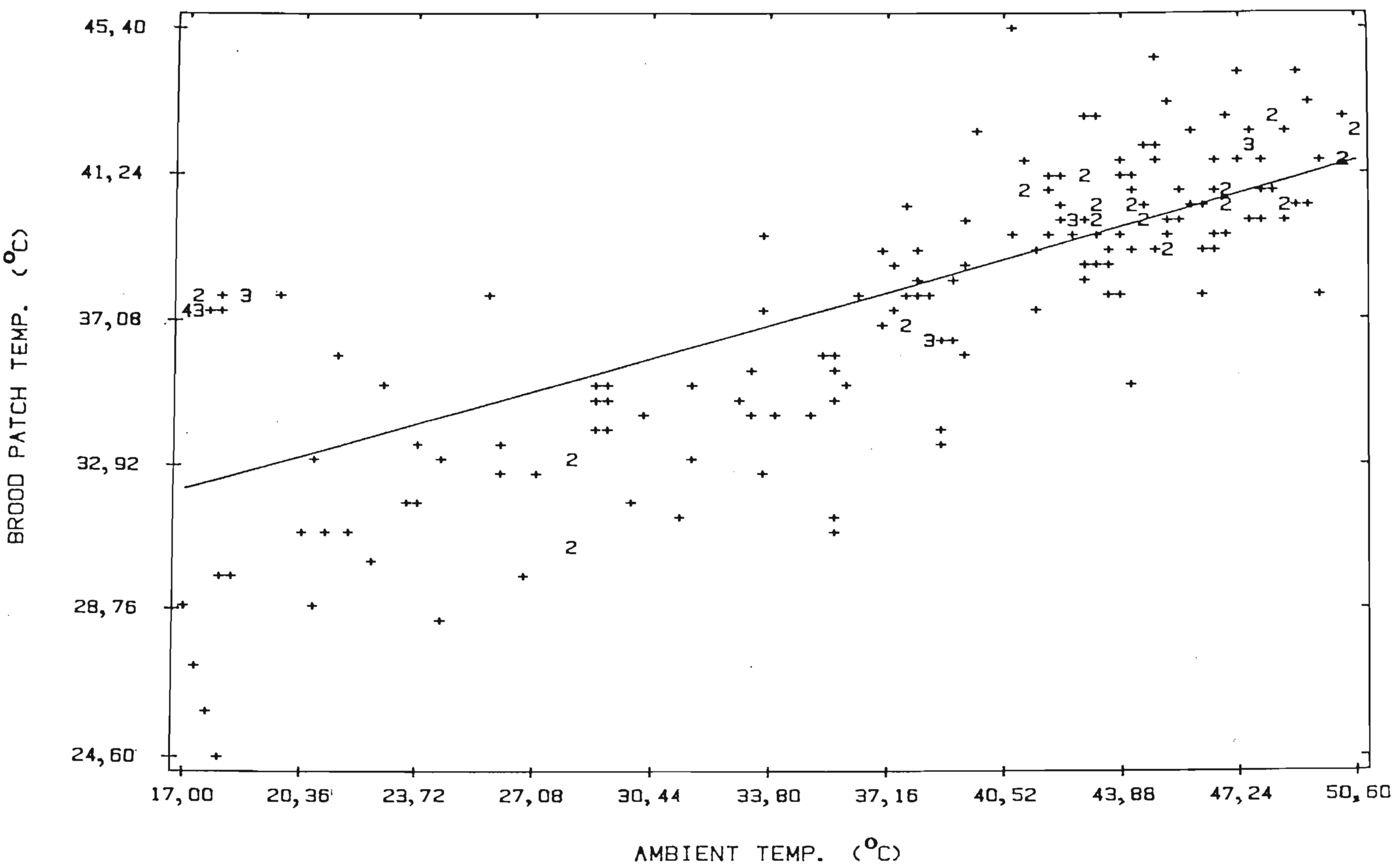


Fig. 4.29. Relationship between brood-patch temperature and ambient temperature in three Lesser Blackwinged Plover pairs at Ndumu. Best-fit curve is $y = 27,42 + 0,28x$; $\underline{r}^2 = 0,53$; $p < 0,01$; $n = 195$. Number indicate the number of coinciding temperature values.

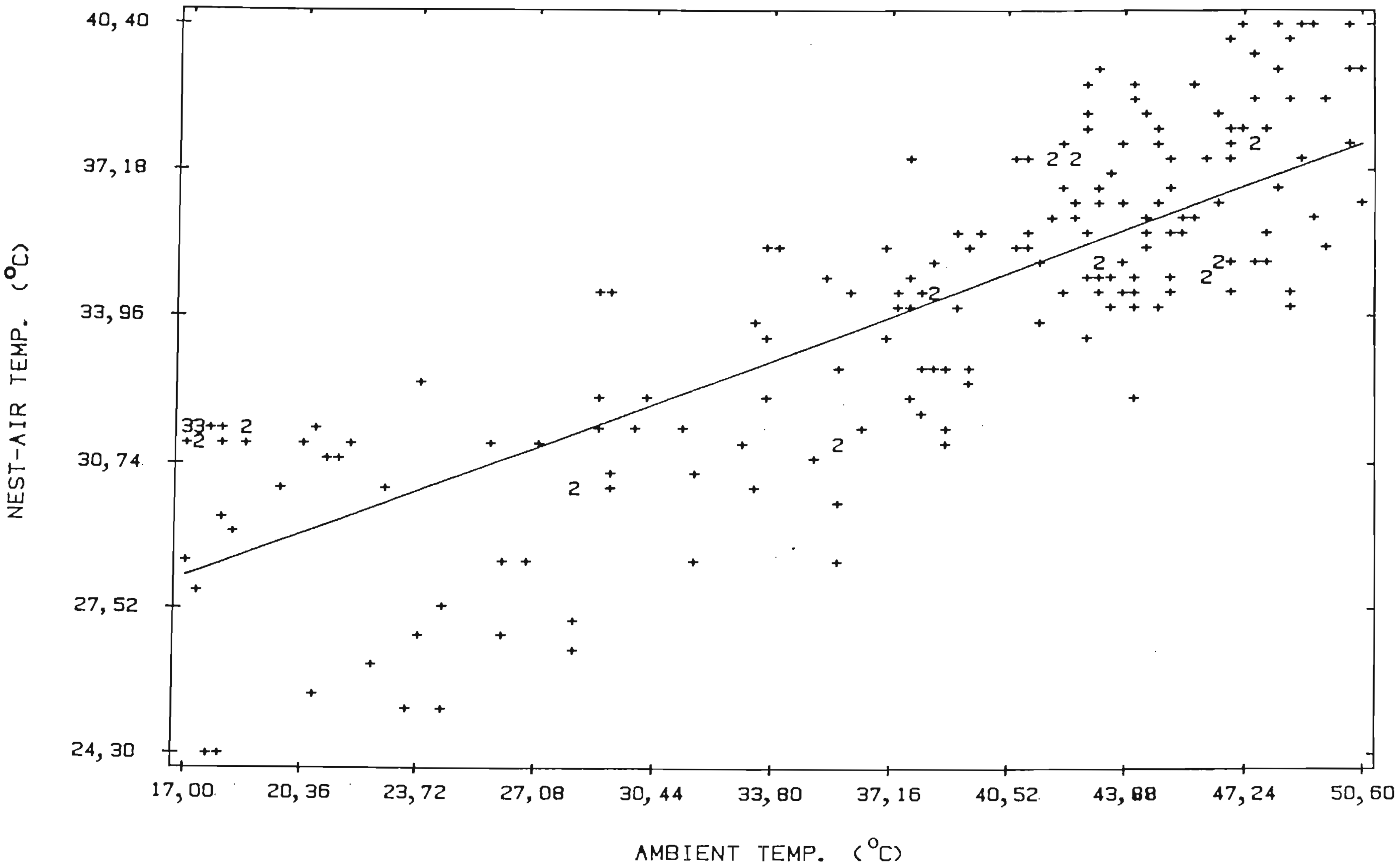


Fig. 4.30. Relationship between nest-air temperature and ambient temperature in three Lesser Blackwinged Plover pairs at Ndumu. Best-fit curve is $y = 23{,}69 + 0{,}28x$; $\underline{r}^2 = 0{,}65$; $p < 0{,}01$; $n = 195$. Numbers indicate the number of coinciding temperature values.

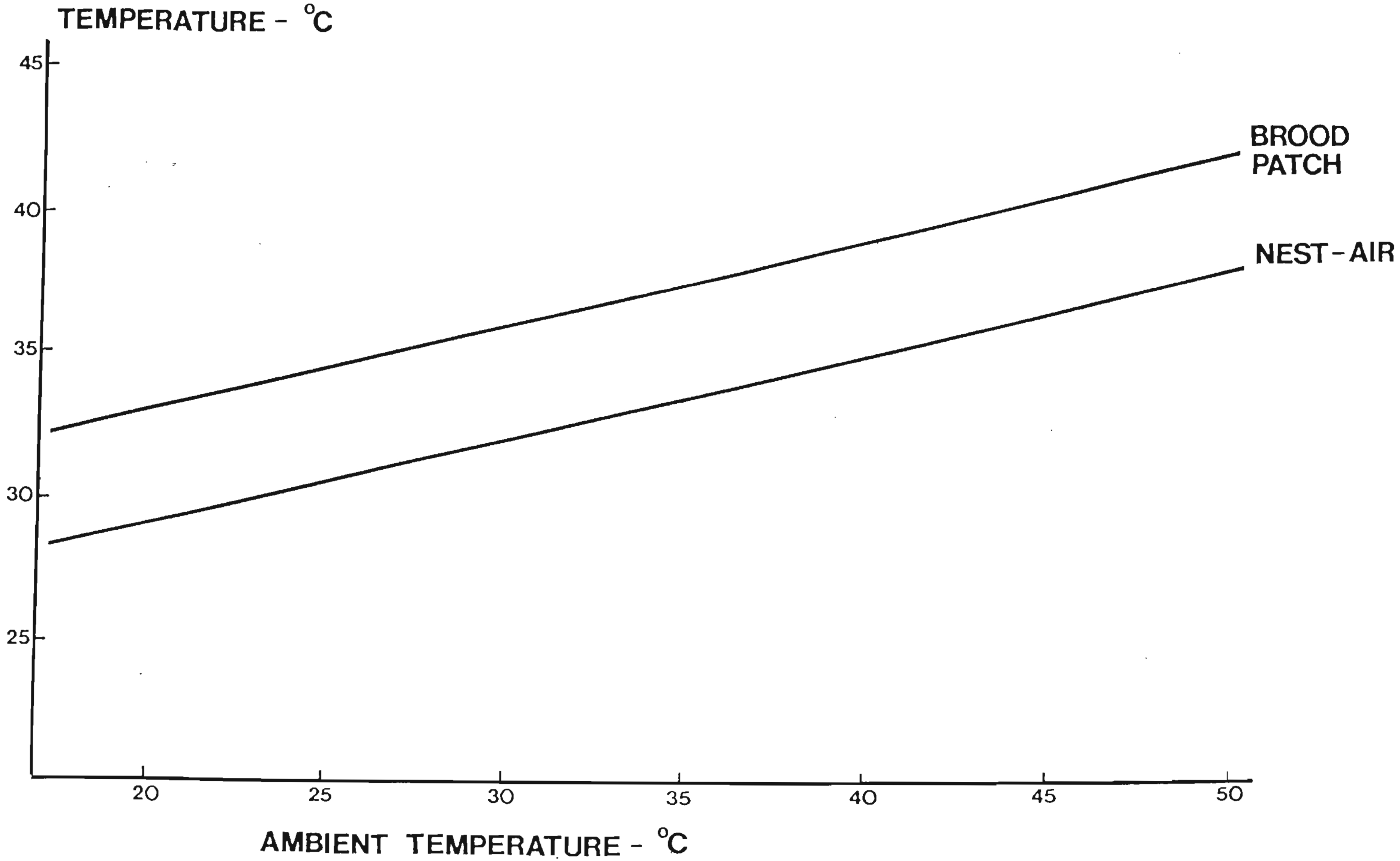


Fig. 4.31. Relationship between brood-patch and nest-air temperature and ambient temperature in three Lesser Blackwinged Plover pairs at Ndumu to demonstrate the gradient over the egg caused by the difference between brood-patch and nest-air temperature. Best-fit curves as for Figs 4.29 and 4.30

period, reaching a maximum in the >40 °C category (Fig. 4.32). Mean incubation-bout duration decreased significantly at temperatures above 40 °C. Mean incubation-bout duration in this species was 40,12 ±4,15 min (Fig. 4.33). Males controlled incubation in this species, relieving females at the nest without females vocalizing while females responded to males' soft, low frequency tiu calls (not tape-recorded) for nest relief. These calls were given intermittently for about 1 min before the off-duty parent responded. The off-duty bird then walked up to the nest, stood about 10 cm from it and waited for the incubating bird to stand up. The on-duty bird stood and started sideways-throwing immediately without moving away from the nest. This sideways-throwing was more vigorous than in Crowned and Blackwinged Plovers, since the bird threw small pieces of grass for up to 20 cm at a time. The incoming bird sat down virtually under the tail (if it approached from the back) or under the belly (if it approached from the front) of the departing bird, which continued to sideways-throw for about 1 min after being relieved. Thereafter, the relieved bird moved off to stand in the shade.

Nest attendance increased in Lesser Blackwinged Plovers at temperatures above 40 °C (Fig. 4.34). They vacated the nest in the mornings but not in the afternoons to feed. Six pairs nesting together in a loose colony in Ndumu in 1985 all left the nesting area simultaneously each morning to feed at Mandlankunse pan (Introduction - Fig. 5) about 5 km south of the breeding area at

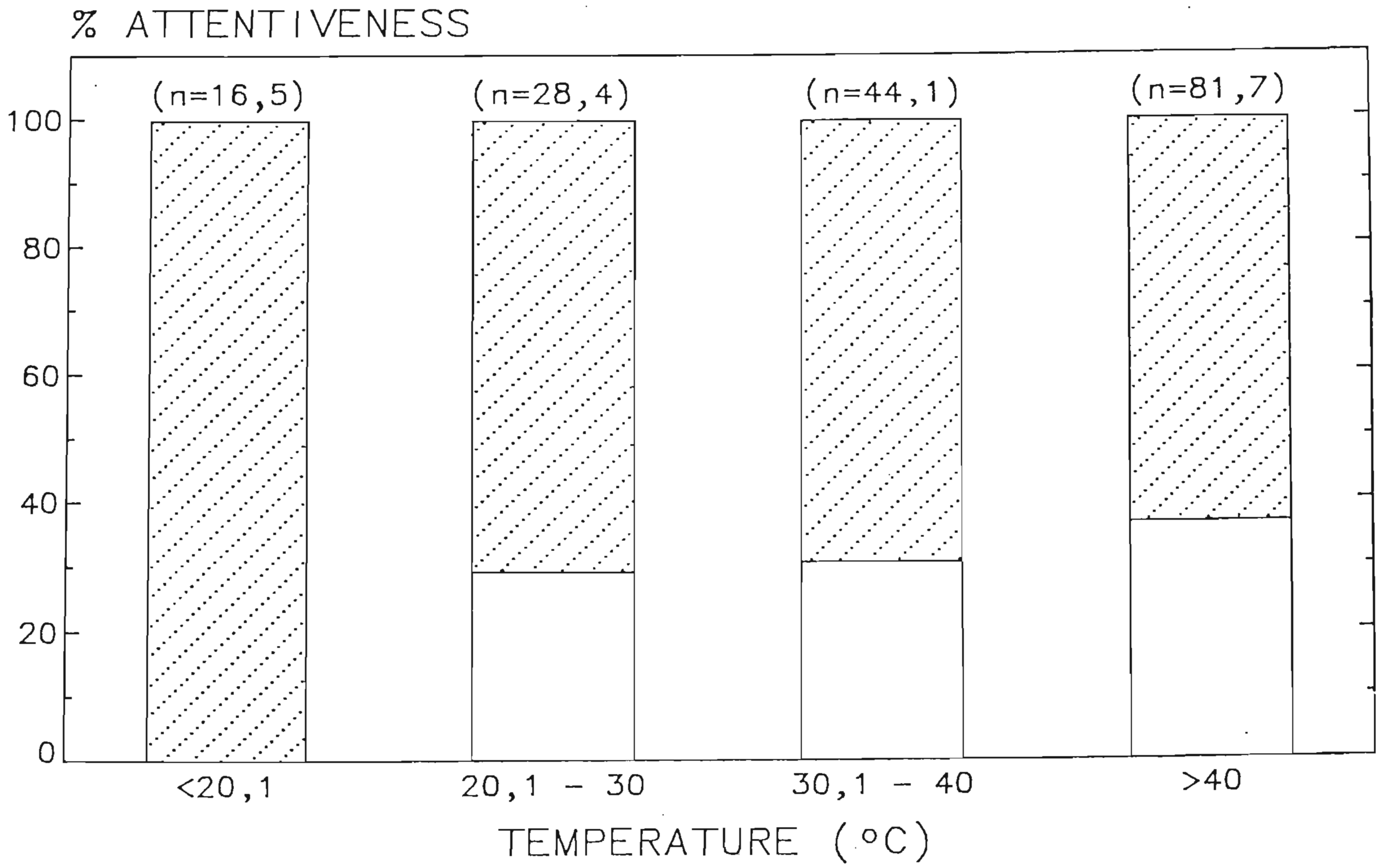


Fig. 4.32. Lesser Blackwinged Plover: nest attentiveness measured as a percentage of total time spent by male and female on the nest in each temperature category, for three pairs at Ndumu. n = number of hours of observation in each temperature category. Shaded area = female; unshaded = male.

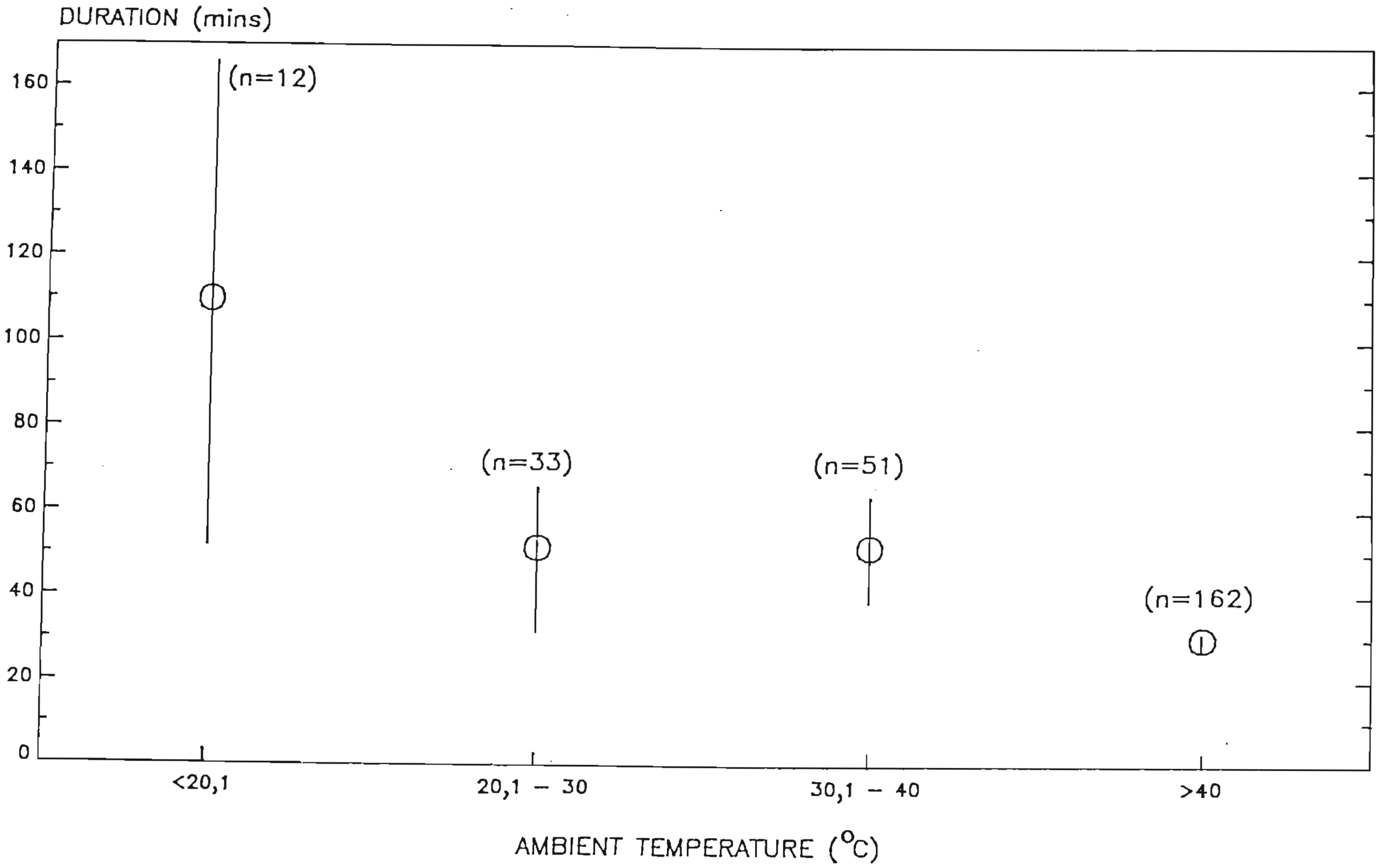


Fig. 4.33. Lesser Blackwinged Plover: incubation bout duration in three pairs at Ndumu. Means (o) and 95% confidence limits (vertical lines) are plotted. n = number of incubation bouts observed in each temperature category.

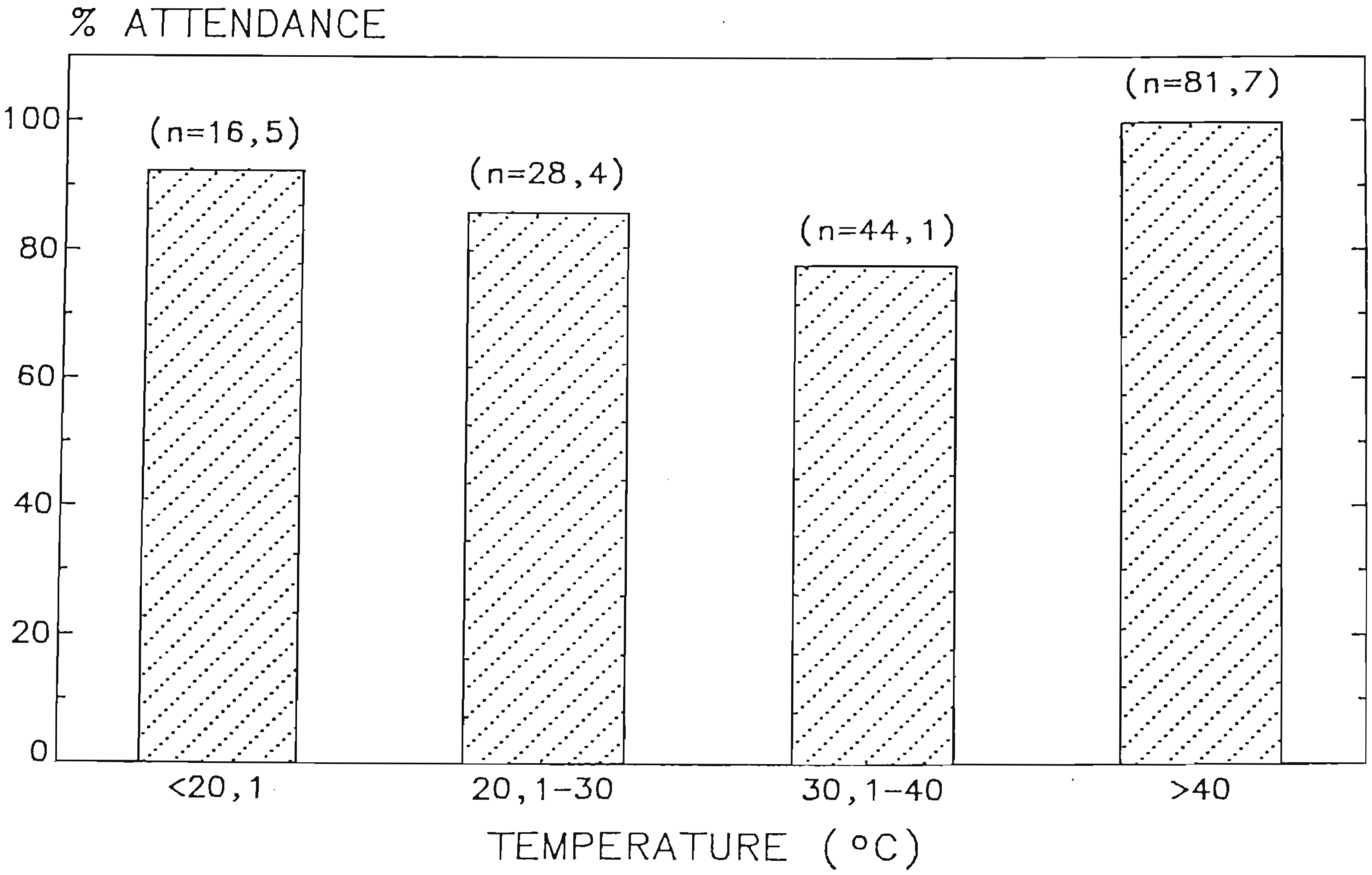


Fig. 4.34. Lesser Blackwinged Plover: nest attendance measured as a percentage of total time spent observing three pairs at Ndumu. n = number of hours of observation in each temperature category.

Bunguzane in Ndumu Game Reserve. Shading behaviour in Lesser Blackwinged Plovers was done much less at high temperatures than was the case in Crowned and Blackwinged Plovers (Fig. 4.35). Lesser Blackwinged Plovers did not shade their eggs at temperatures below 40 °C and shaded the eggs for only 31,2% of the time at ambient temperatures above 45 °C. Lesser Blackwinged Plovers started gular fluttering at 43,0 °C. Feather-ruffling started at 36,7 °C while panting started at 39,8 °C. Lesser Blackwinged Plovers exuded a saline secretion (determined by taste) from the nostrils at temperatures above about 35 °C. At temperatures above about 45 °C, Lesser Blackwinged Plovers were found to have wet legs. This secretion was tasteless and left no exudate upon drying, and therefore did not appear to be urine.

Nest defence

Nest defence took a number of forms and varied both with stage of incubation, time of day/temperature (cf. reactions of Crowned Plovers to Pied Crows in Ndumu - Fig. 4.36) and type of potential predator. Crowned and Blackwinged Plovers reacted in similar ways to predators. If threatened during the cooler periods of the day (ambient temperature less than about 25 °C) they mobbed humans, avian predators, carnivorous mammals and reptiles by flying at them (in mixed-species flocks if nesting in mixed colonies), uttering a kweep-kweep-kweep call (Crowned Plover - Fig. 4.2d) or a ti-ti-ti call (Blackwinged Plover - not tape-recorded) after they passed the intruder. They occasionally

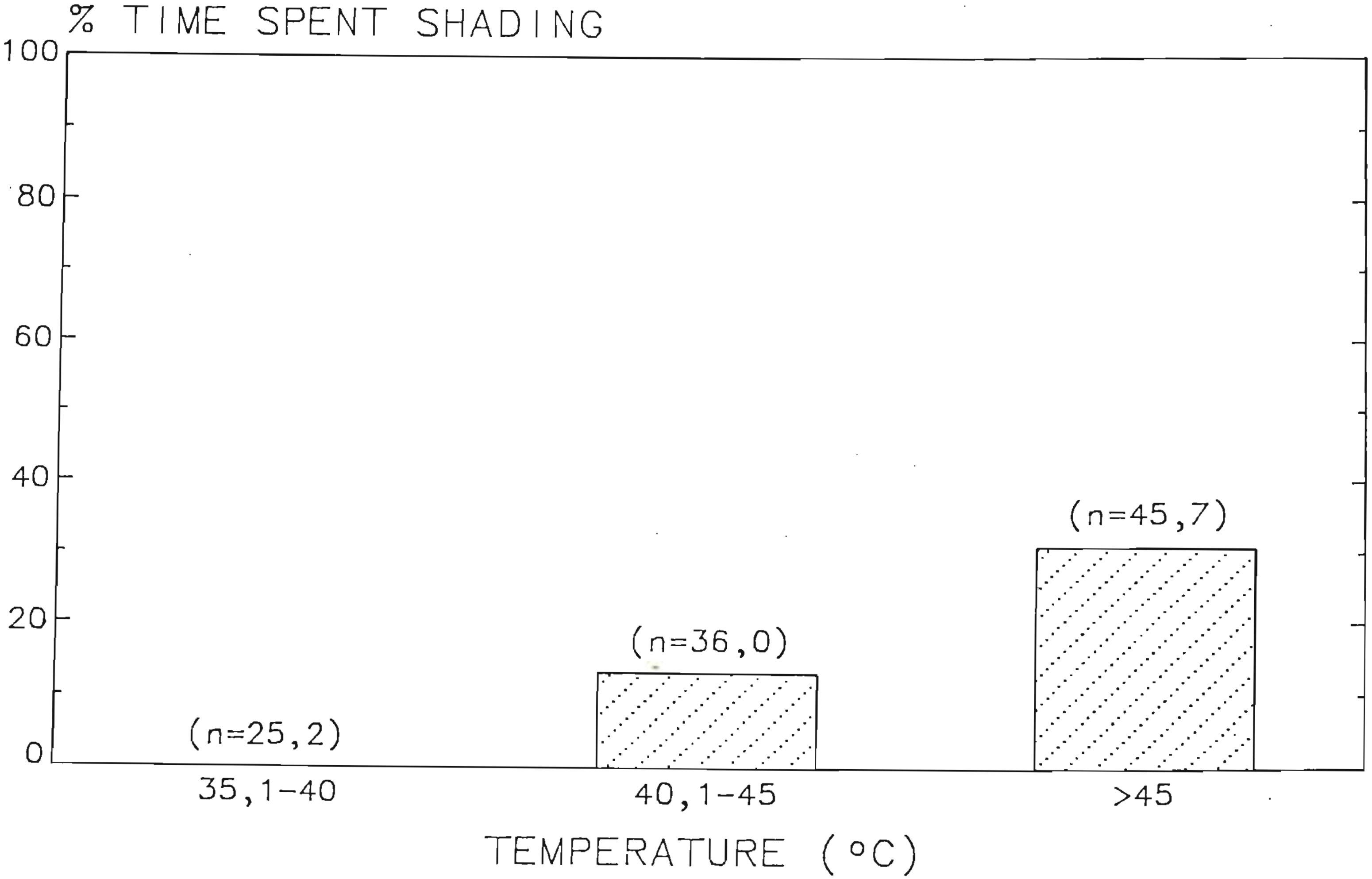


Fig. 4.35. Lesser Blackwinged Plover: time spent shading eggs measured as a percentage of total time spent observing three pairs at Ndumu. n = number of hours of observation in each temperature category.

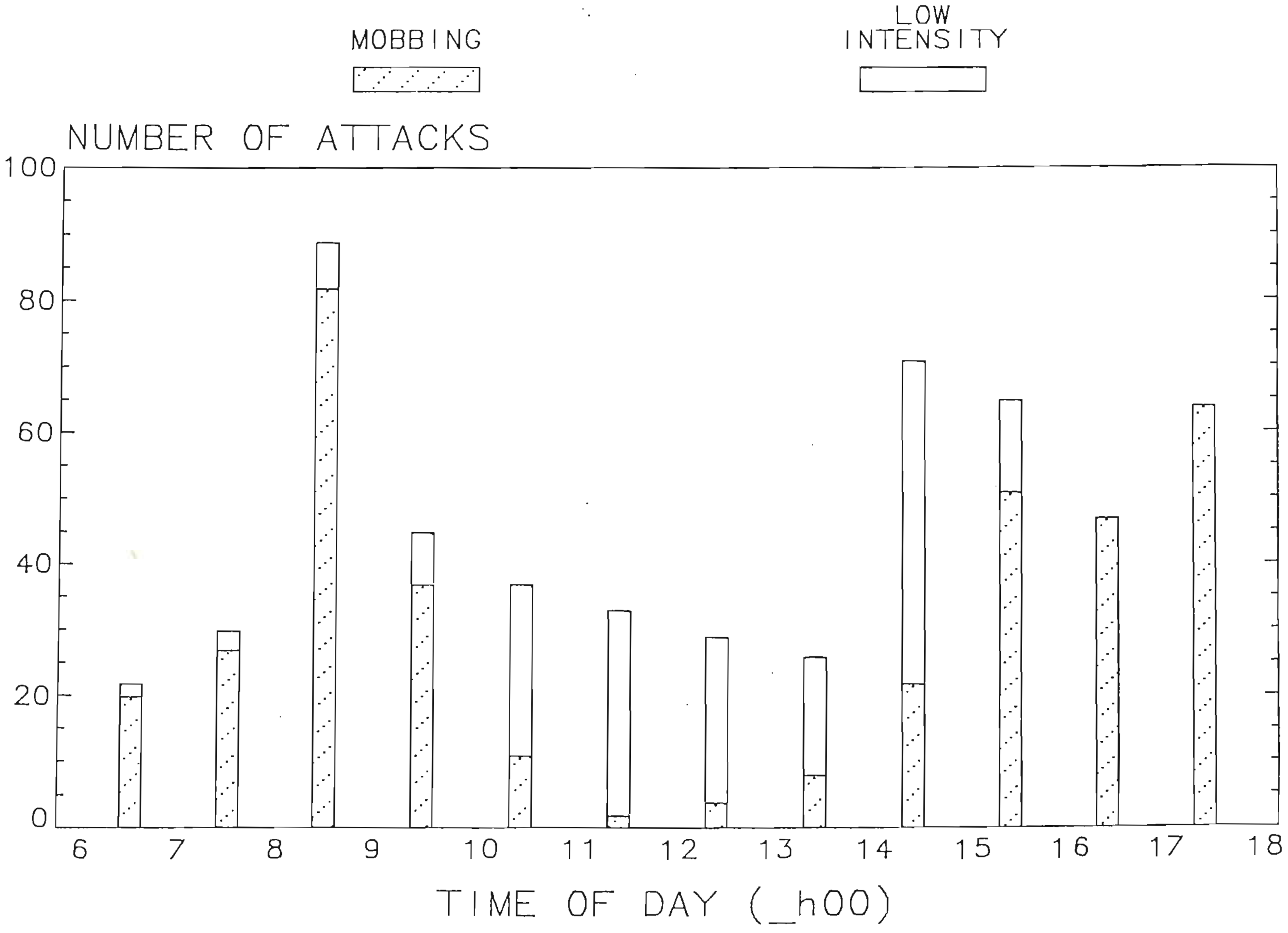
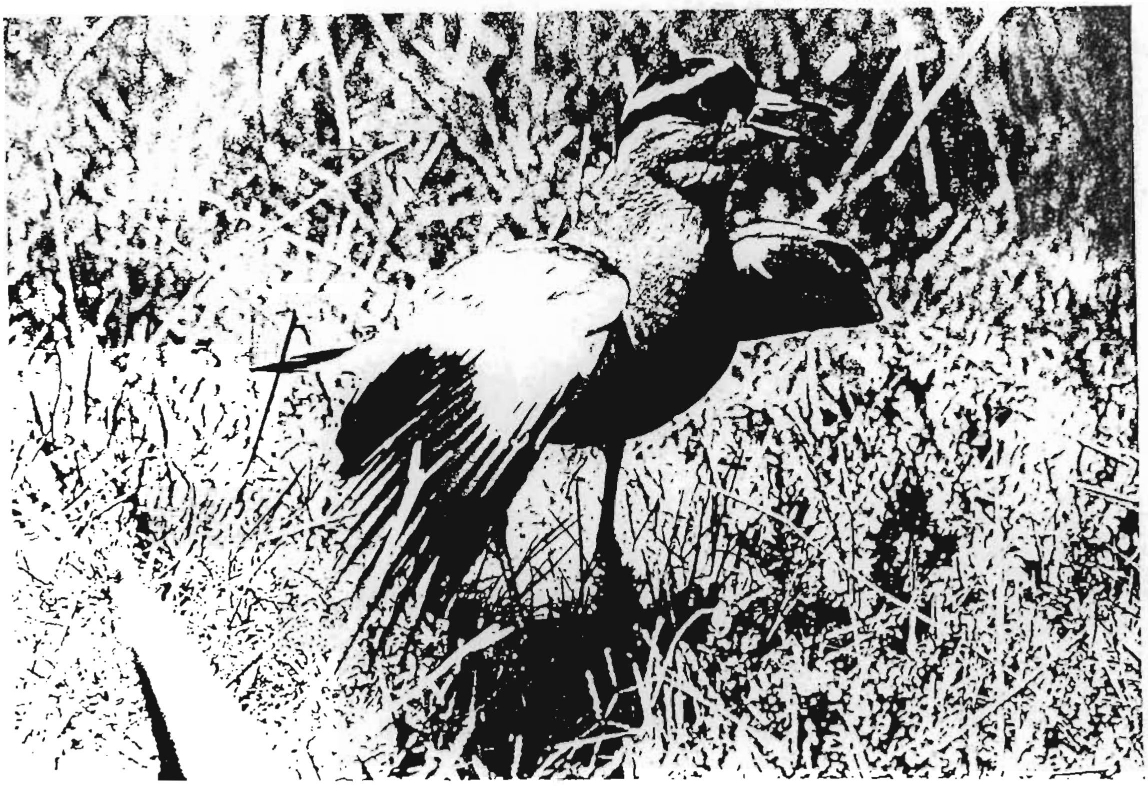


Fig.4.36. Reactions of Crowned Plovers to attacks by Pied Crows Corvus albus at Ndumu Estates from 01 June-16 June 1986.

dropped their legs or very rarely used a wing to strike the intruder. Blackwinged Plovers never went closer than about 2 m to an intruder in these mobbing attacks. If the intruder did not move off after persistent mobbing attacks, both species returned to the ground and flapped one or both outstretched wings on the ground with one or both wingtips lifting 3-5 cm off the ground at each flap (Figs 4.37a and b). They also held the hand folded and flapped the wings away from the body. In both ground displays, the belly touched the ground and the tail was folded. A third ground display involved spreading both wings out laterally and fanning the tail and rushing at the intruder. A fourth ground display, which was performed by both Crowned and Blackwinged Plovers from the onset of aggressive behaviour in April 1985 and 1986, was false-brooding. This display involved squatting down as if on a nest while the partner called loudly (this display was performed before laying by paired birds only). All of the abovementioned displays were performed regardless of the time of day in the last five days before hatching of the eggs.

If threatened during the hotter part of the day, Crowned Plovers walked off the nest and began uttering a low-intensity wiit-wiit call (not tape-recorded), which increased in intensity as the intruder approached. The intruder was mobbed if it approached within 5 m of the nest.

Incubating Blackwinged Plovers lay flat on the nest and kept their heads at the same height as the rest of the body if an a)



b)

Fig. 4.37. Distraction displays of Crowned Plover: (a) Low intensity display, (b) High intensity display. Photos: C. Urquhart.

avian predator flew over during the hotter part of the day, while the off-duty parent remained silent. If the intruder approached to within about 10 m of the nest, Blackwinged Plovers then stood up and flew off, alighted at least 30 m away and proceeded to utter the *ti-ti-tiree* alarm call (not tape-recorded). Blackwinged Plovers mobbed avian predators at this time of day only if they continued to hover over the nest after the plovers had vacated it. If a terrestrial predator approached, the off-duty bird would attack it using the spread-and-fanned-tail display, while the incubating bird crouched low on the nest; it left the nest and helped the off-duty bird to attack the intruder only if the latter were unable to repulse the intruder.

Most predators of the three study species were avian, although a mongoose and a snake were also recorded as predators during the study period (Table 4.2). Crowned Plovers could discriminate between potential predators and non-predators among the Falconiformes, since they did not become alarmed at the presence of adult Bateleurs *Terathopius ecaudatus*, Blackbreasted Snake Eagles *Circaetus pectoralis* and Lizard Buzzards *Kaupifalco monogrammicus*, all of which did not attack the plovers. Crowned Plovers did become alarmed at the presence of immature Bateleurs, which did attack the plovers' chicks (Table 4.2). Blackwinged and Lesser Blackwinged Plovers treated all raptors as potential predators.

The response of Crowned, Blackwinged and Lesser Blackwinged

Table 4.2. Predators of Crowned, Blackwinged and Lesser Blackwinged Plovers.

PREDATORS	ADULTS	CHICKS	EGGS
Scopus umbretta		CP_7/BP_3	CP_{11}/BP_4
Terathopius ecaudatus		CP_{17}/LBP_5	
Accipiter badius		CP_{11}	
Falco biarmicus	CP_{47}/BP_{43}		
Micronisus gabar		CP_2/LBP_7	
Polyboroides typus			CP_{28}/BP_4
Sagittarius serpentarius		CP_{19}	CP_{27}
Circus ranivorus	CP_{13}/BP_{12}	CP_4/BP_1	
Asio capensis	CP_2		
Tockus alboterminatus		CP_9	CP_3
Corvus albus		CP_{619}/BP_{23} LBP_6	CP_{46}/BP_3 LBP_5
Corvus capensis		BP_{46}	BP_{37}
Galerella sanguinea [a]			LBP_2
Dasypeltis scabra [b]			LBP_2

CP = Crowned Plover; BP = Blackwinged Plover; LBP = Lesser Blackwinged Plover. Subscript numbers indicate the number of observations of predatory attempts on that species. [a] = class Mammalia; [b] = class Reptilia.

Plovers to large herbivorous mammals approaching close to the nest was to sit on the nest until the herbivore was 20-30 cm from the nest and then to stand up quickly and spread the wings, fan the tail and utter a noisy weep-weep-weep call (Crowned Plovers - Fig. 4.2c) or a tiree-tiree call (Blackwinged Plovers - Fig. 4.3a) or a ti-huh call (Lesser Blackwinged Plovers - Fig. 4.3b), which was enough to turn the intruder away from the nest.

Lesser Blackwinged Plovers never mobbed or attacked intruders during the incubation period. They remained silent and the sitting bird crouched down on the nest with its head lowered when avian predators flew over. If a terrestrial predator approached, both birds either ran away from the nest and started uttering a ti-huh call (Fig. 4.3b) about 20 m from the nest or the sitting bird would remain on the nest and then fly off uttering a rising, fast ti-ti-ti-ti call (Fig. 4.3d) when the predator was about 10 m away.

Chick-tending behaviour

Chicks of the same clutch hatched within 4-6 hrs of one another in all three species even though eggs were laid at least one day apart. The chicks remained in the nest until their neonatal down had dried (about 4 h). Thereafter, the chicks got up and ran about after their parents. In all three species the parents removed the eggshells from the nest as soon as a chick had hatched. The parent (female in Crowned and Blackwinged Plovers and male in Lesser Blackwinged Plover) then ran about 20-30 m from the nest and broke up the shell with the bill, spreading over an area of ±4 m^2. Broken eggs were also removed and dealt with in the same way as hatched eggs.

All three species shaded the chicks during the heat of the day by squatting over them for the first week after hatching. Thereafter, chicks were led to a shady tree once the ambient temperature rose above about 28 °C. At temperatures higher than about 30 °C, all three species' chicks exuded a saline solution (determined by taste) from the nostrils. Chicks were shown food items by the parent birds in all three species, the parents taking turns to tend the chicks in order to allow the off-duty parent to feed. In the case of predators being present, the chicks split into two groups of approximately equal size, each of these groups following one of the parents. Parents in all three species mobbed predators while the chicks ran and hid under any concealing vegetation. Chicks remained under cover until the parents uttered the low-pitched krr-krr all-clear call (not tape-recorded). The chicks of all three species remained with the parents for about a year, and left the parents before the onset of the following breeding season in the case of Blackwinged and Lesser Blackwinged Plovers. Crowned Plover chicks remained with the parents if the parents had another clutch before the chicks were a year old (n = 3) and helped the parents defend the new clutch and brood against predators by engaging in aerial mobbing along with the parents.

Chick growth

Growth curves were derived for Crowned and Blackwinged Plover chicks until they started to fly (Figs 4.38 and 4.39). Neither species' weights reached an asymptote during this period. The growth of the tarsi and culmen of Crowned and Blackwinged Plovers were also plotted (Fig. 4.40a and b; Fig. 4.41a and b). Five Lesser Blackwinged Plovers weighed 8 g each at hatching. Crowned Plovers took an average of 30 days to reach flying age while three Blackwinged Plovers were 29, 31 and 31 days old when they first flew. The heaviest non-flying Crowned Plover was 125 g while the heaviest Blackwinged Plover was 126 g. No Lesser Blackwinged Plovers were measured at flying age.

Chicks of all three species started losing the down feathers from about 7-8 days of age. Down was replaced by contour feathers on the wing coverts first, the primary and secondary remiges then started to erupt, followed by the rectrices. By the time they started to fly all three species had replaced all down feathers except those on the intrascapular area. Flight was achieved only once the rectrices had developed, the remiges having become suitable for flight about five days earlier. Fledged chicks of all three species retained buff edges to all the brown feathers for about one year.

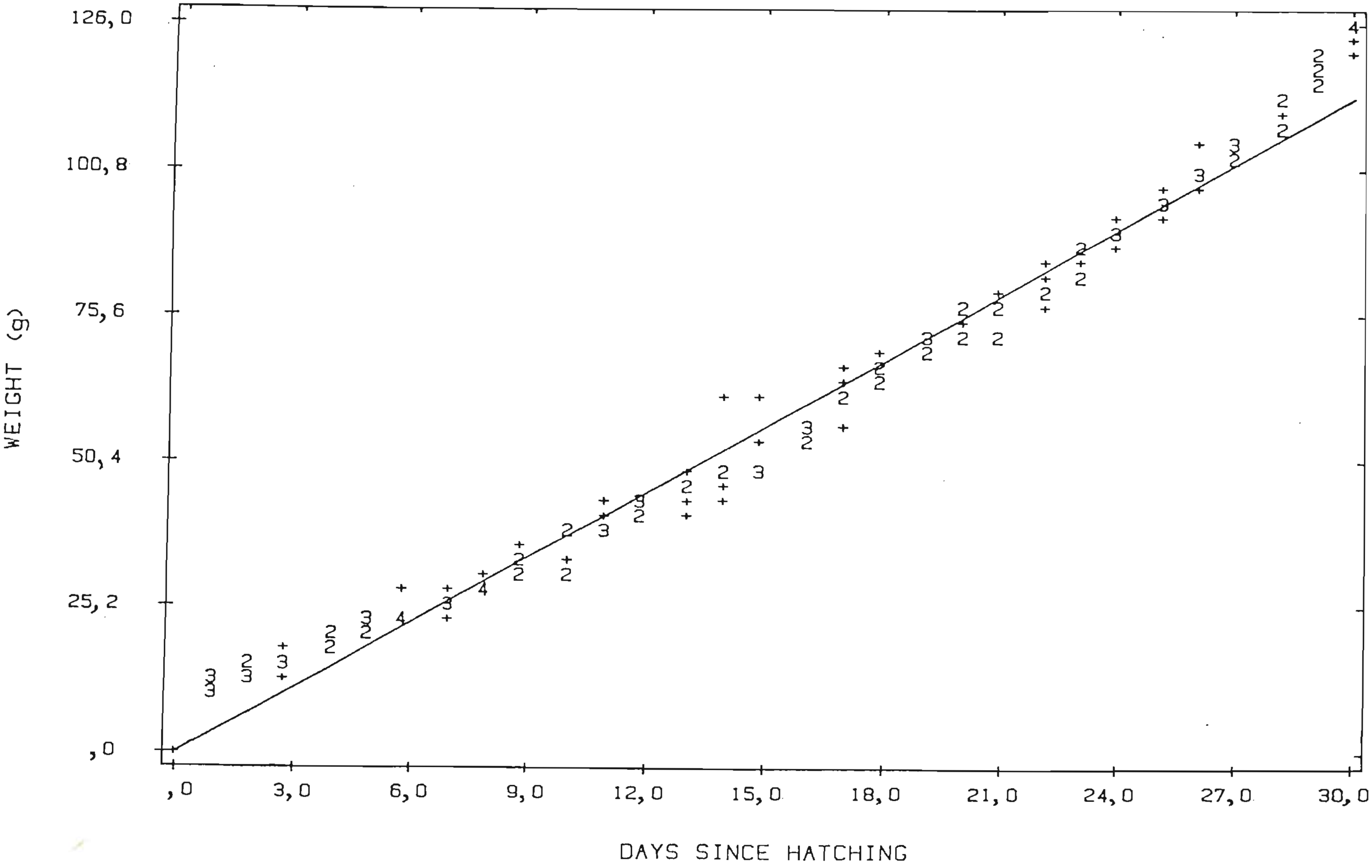


Fig. 4.38. Growth rate of Crowned Plover chicks measured as weight increase until flight was achieved. Best-fit curve is $y = 1,2077 + 3,7502x$; $\underline{r}^2 = 0,98$; $p < 0,05$; $n = 153$. Numbers indicate the number of chicks with the same weight at a specific age.

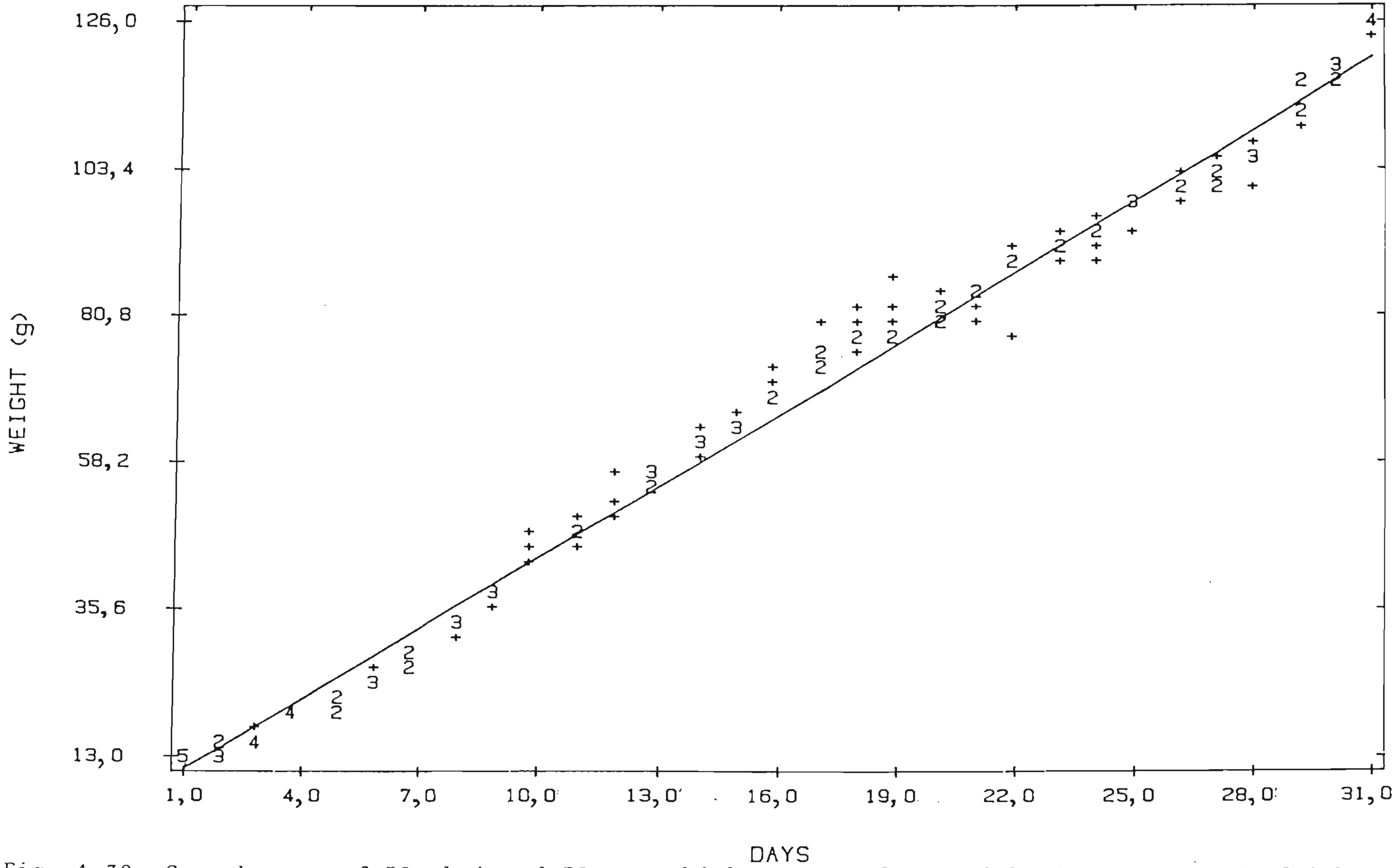


Fig. 4.39. Growth rate of Blackwinged Plover chicks measured as weight increase until flight was achieved. Best-fit curve is $y = 7{,}59 + 3{,}64x$; $\underline{r}^2 = 0{,}99$; $p < 0{,}05$; $n = 137$. Numbers indicate the number of chicks with the same weight at the same age.

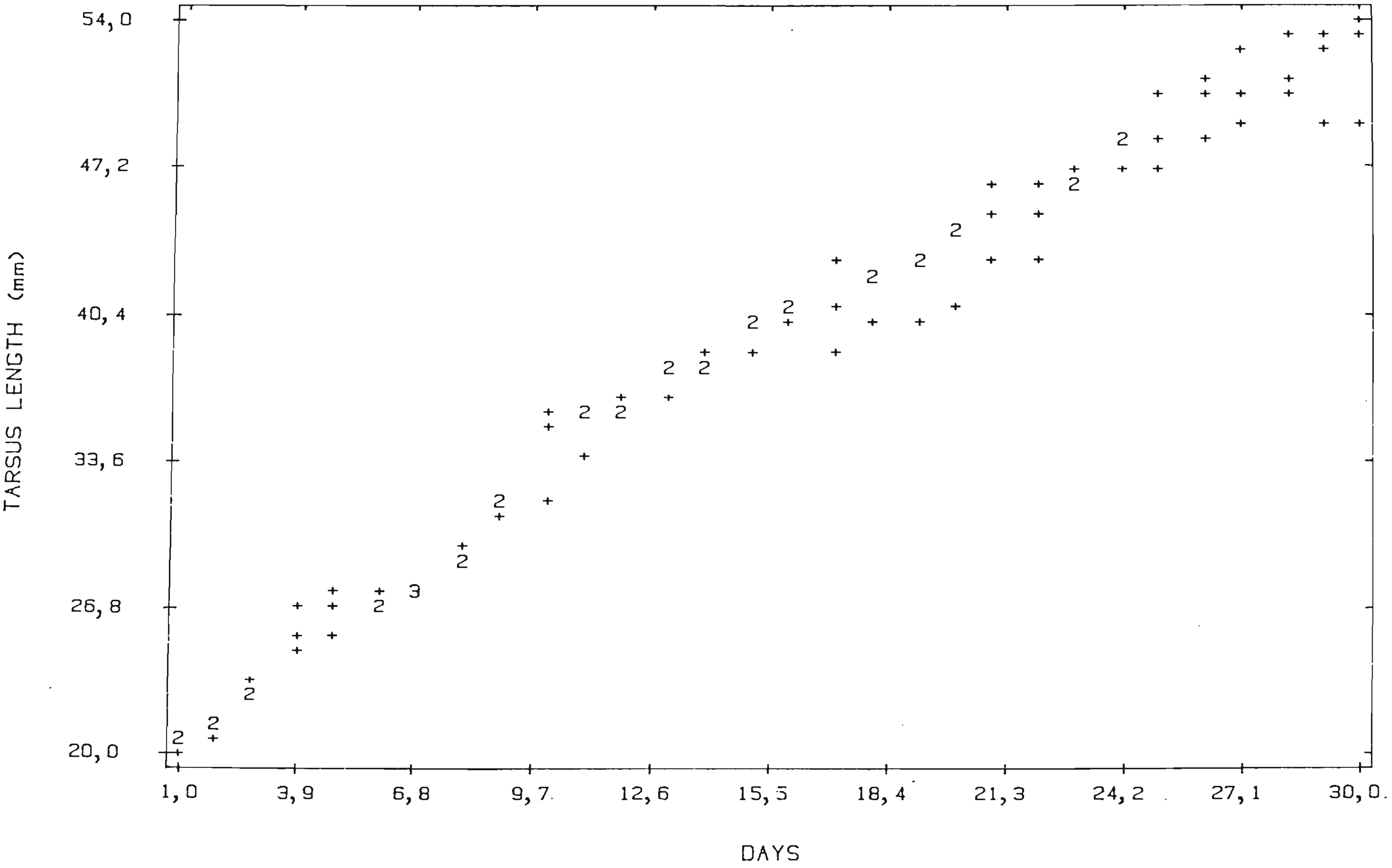


Fig. 4.40a. Growth of Crowned Plover tarsi from hatching to flying age (30 days). Numbers indicate the number of chicks with the same tarsus length at the same age.

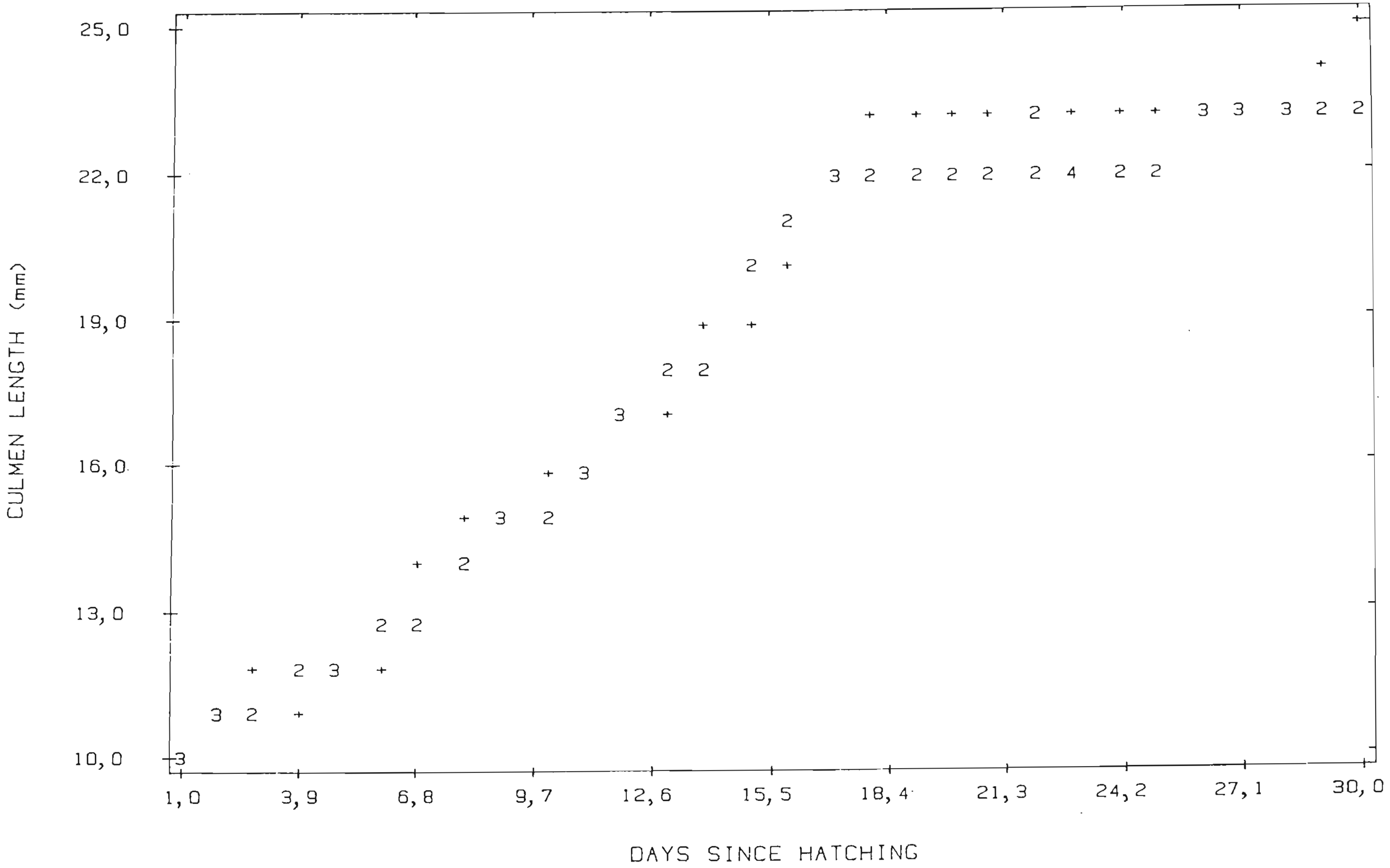


Fig. 4.40b. Growth of Crowned Plover culmen from hatching to flying age. Numbers indicate the number of chicks with the same culmen length at the same age.

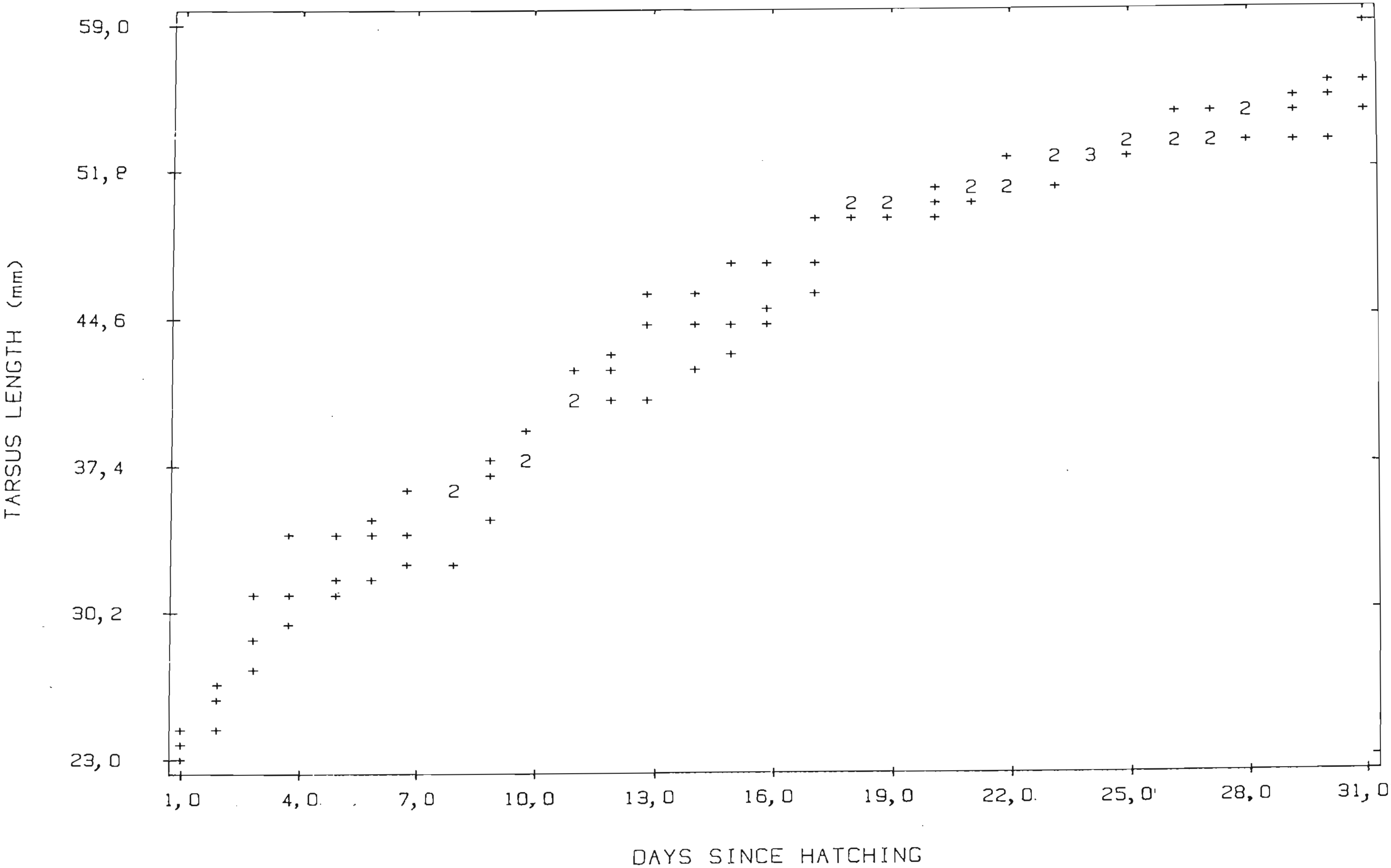


Fig. 4.41a. Growth of Blackwinged Plover tarsus from hatching to flying age. Numbers indicate the number of chicks with the same length tarsi at the same age.

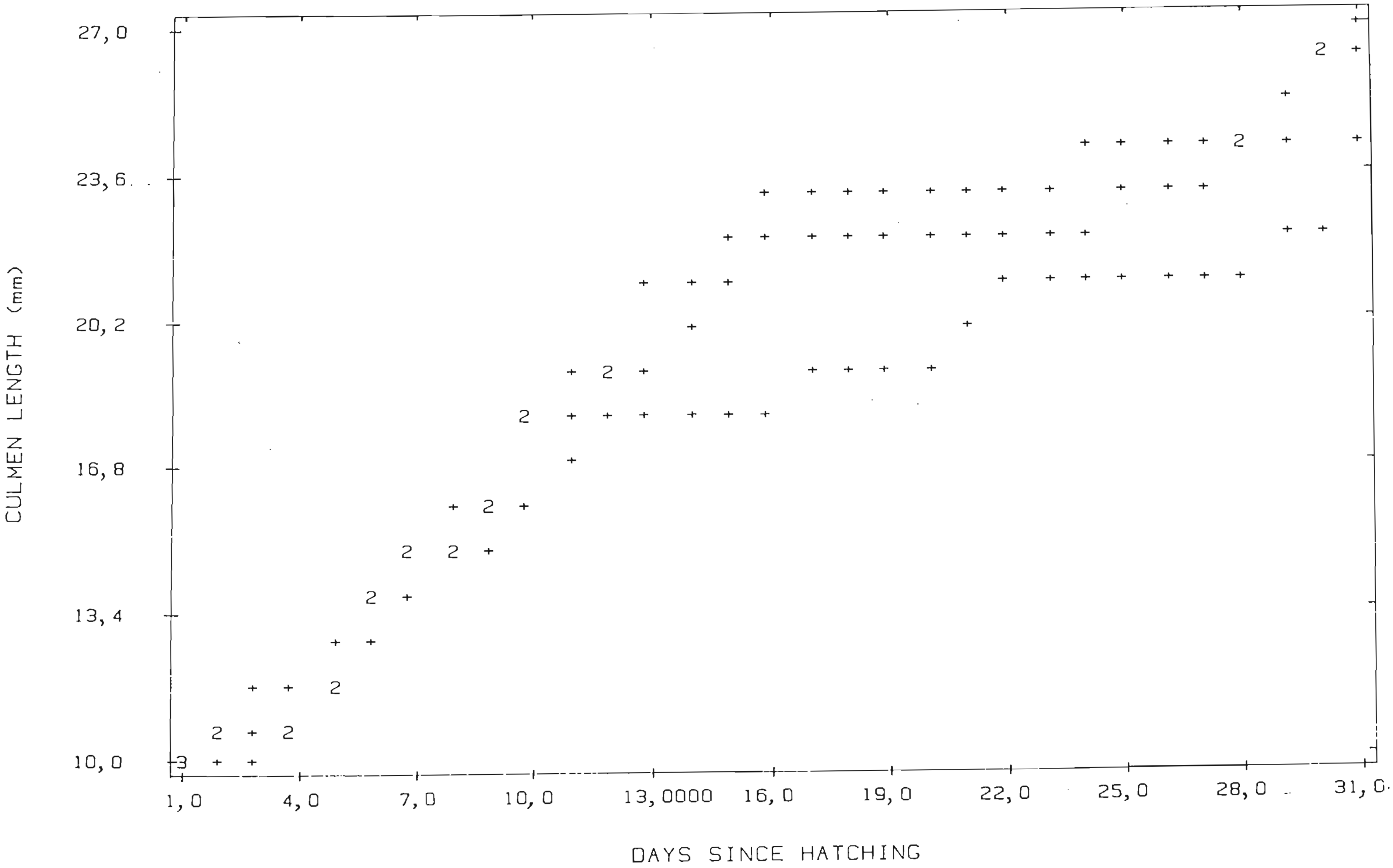


Fig. 4.41b. Growth of Blackwinged Plover culmen from hatching to flying age. Numbers indicate the number of chicks with the same culmen length at the same age.

The ontogeny of the calls of the Crowned Plover are detailed in sonagrams in Figs 4.2a and 4.2b. Crowned Plover chicks initially produced a short cheeping call which has a wide range of frequencies (exceeding 8 kHz) (Fig. 4.2a). This call then reduced in frequency, but retained virtually the same amplitude and duration until the chicks were able to fly (see sonagram of 30-day-old chick - Fig. 4.2b). The adult call (Fig. 4.2c) was not produced before the chicks could fly.

Reproductive success

Reproductive success in Crowned, Blackwinged and Lesser Blackwinged Plovers in the study areas in 1985 and 1986 is documented in Table 4.3. These results are higher than those determined for Blackwinged Plovers at Scottsville Racecourse in December 1986 by counting the numbers of immature birds relative to the number of adults (fledging success = 32,2%), while results for Crowned Plovers taken at Scottsville Racecourse in December 1986 are higher than those shown in Table 4.3 (fledging success = 58,7%).

DISCUSSION

Mate acquisition and territorial behaviour

The onset of aggression and sexual behaviour in Crowned and

Table 4.3. Reproductive success of Crowned, Blackwinged and Lesser Blackwinged Plovers.

Year	Clutches laid	Eggs laid	Eggs hatched	% Hatching success	Survived to flying	% Reproductive success to flying
Crowned Plover						
1985	10	26	21	80,8	14	54,0
1986	43	102	80	78,4	57	52,0
Blackwinged Plover						
1985	4	12	11	91,7	9	75,0
1986	14	42	42	100,0	33	78,6
Lesser Blackwinged Plover						
1985	16	54	40	74,1	30	55,6
1986	9	26	11	42,3	10	38,5

Blackwinged Plovers in April, several months before the onset of breeding in August and September and concomitant with the drop in food availability with the onset of winter, allows these species the opportunity to breed immediately should a flush of prey items occur. Crowned Plovers did breed in response to a flush of prey items at Ndumu in May 1986. Breeding has been recorded in this species throughout the year (Chapter 5, Fig. 5).

None of the study species nested in the same place in 1986 as they did in 1985 unless the territories were maintained with short grass, either by mowing or by overgrazing. This use of a short-grass habitat may be required because the long, thin legs of these birds are unable to propel them over unstable or uneven surfaces or because they are unable to detect or capture food items in long grass. This requirement of short grass means that, under natural conditions, it is unlikely that they would be able to maintain territories over long periods of time. It is probably for this reason that Crowned and Blackwinged Plovers initiate aggressive and sexual behaviour many months before they may breed, so that they can breed immediately once they find a suitable breeding habitat with a large enough food supply to maintain them.

Nest site selection

Blackwinged and Lesser Blackwinged Plovers prefer burnt ground because it affords crypsis. Many Blackwinged Plovers nested near raised objects to improve the crypsis of the adult and, therefore, the nest, while Lesser Blackwinged Plovers nested in woodlands so that trees would obscure the bird and nest from a predator's view. Crowned Plovers, whose eggs have a khaki ground colour (hue 5Y, value and chroma 8/2 - Munsell 1966), rather than brown (hue 5Y, value and chroma 6/4 - Munsell 1966) as in the other two species, prefer to lay in unburnt grass because the eggs are more cryptic there. However, all three species will lay in either burnt or unburnt grass, because the less favoured type still affords the eggs a great degree of camouflage and the preferred habitat type is not always available. Blackwinged Plovers lay in longer, dense grass and not in short, unburnt grass when burnt grass is unavailable (they also do this in the eastern Cape (Butcher 1984, MS)) perhaps because of the apparent abundance of this type of grass in the highland regions which cover much of their range (as opposed to short grass of low basal cover used by Crowned and Lesser Blackwinged Plovers). The use of longer grass has become imprinted and even where short grass of low density is available (such as in Pietermaritzburg), it is not used. The fact that Crowned and Lesser Blackwinged Plovers use short sparse grass is probably a result of the abundance of short grass of this type over their ranges.

All three species usually nested in loose colonies which may enhance antipredator behaviour such as early warning (Lack 1954, Pulliam 1973), predator detection (Hamilton 1971) and mobbing behaviour (Andersson 1976, Montevecchi 1977) although it may result in competition for food (Lack 1968, Ogden 1978), nest sites (Orians 1961) and mates (Mock 1976, Hunt 1980). The advantages of colonial nesting mentioned above are all demonstrated in the three species (especially Crowned and Blackwinged Plovers which are active mobbers of predators at all stages). In all three species, intraspecific competition for food in nesting colonies was largely avoided by the use of feeding grounds away from the breeding areas, the most exceptional of which was the group of Lesser Blackwinged Plovers which flew about 5 km each day to obtain food. Hockey (1982) has observed this "leapfrogging" behaviour in African Black Oystercatchers _Haematopus moquini_ and suggested that nesting territories and feeding territories are not necessarily the same if the feeding sites are unsuitable nest-sites because of the lack of camouflage afforded by the terrain. However, in Crowned and Lesser Blackwinged Plovers this "leapfrogging" occurred because the feeding areas did not have trees or shrubs under which the off-duty bird could rest. Competition for nest sites and mates did occur and may certainly be an important detractant from colony life although not sufficient for the birds to prefer nesting singly.

Nesting in mixed-species colonies is advantageous because there are many birds around to look for food, while at the same time reducing the likelihood of competition for food (when compared with a single-species colony of the same size) because the species are not likely to have exactly the same food preferences.

However, of all the mixed-species colonies seen, only in the association of Redwinged Pratincoles and Crowned Plovers is there a feeding separation because Redwinged Pratincoles are aerial feeders, although their chicks are not. All of the mixed-species nesting associations which included Crowned Plovers were advantageous to those species nesting with them because they are aggressive mobbers of predators. This association is potentially disadvantageous to Crowned Plovers because of interspecific competition for food, although this never occurred because Crowned Plovers took the feeding territories they required and the other species nested near them. The association between Lesser Blackwinged Plovers and Redeyed Doves was more unusual because of the different nesting requirements. However, this association has no disadvantages and has the advantage of the dove being better able to warn the plover of the presence of an avian predator while the plover warned and distracted terrestrial predators such as Slender Mongoose _Galerella sanguinea_ which unsuccessfully attacked both species on two occasions.

"Rapes" observed in Crowned Plovers (also called kleptogamy (Hamilton 1971)) followed the "hawk-dove strategy" predicted by Maynard-Smith (1982) because the intruder ("dove"), who stood to gain by spreading his genes, is submissive once confronted by the territory owner ("hawk") since he would gain nothing from winning a fight with the "hawk" and taking over the female because the "hawk" would no longer look after the "dove's" genes. Kleptogamy is both an advantage and a disadvantage of colonial life; because it is advantageous to a male to spread his genes via as many females as possible but disadvantageous if he is cuckolded and has to incubate eggs and look after young that are not his. It is important to note that Crowned Plovers are the only one of the three species to lay replacement clutches and the only one in which "rape" occurred because it is worth the expense of energy by the male to "rape" a female even if she has eggs, in case she loses that clutch and then lays a replacement clutch.

Nest construction

The construction of a cryptic nest in the three study species is typical of the Charadriiformes (Johnsgard 1981) and necessary in a bird that nests on the ground to prevent detection by predators. Sideways-throwing behaviour enhances the crypsis of the nest by breaking up the outline of the nest. The production of several scrapes has been recorded in many species of Charadriidae (*e.g.* *Charadrius montanus*, Graul 1974; *Vanellus armatus*, Hall 1958; *V. senegallus*, Little 1967) and, as well as being involved in pair-bond behaviour, may distract predators by giving them the impression that the nest has already been deserted. This is enhanced by the false-brooding behaviour which also makes the predator think that a clutch is in a certain place only to find, once the bird is driven off, that nothing is there.

Initiation of egg-laying

The time of laying in the study species indicates that these birds lay their eggs when the grass is still short, but before any increase in the food supply. Egg-laying is also initiated just as daily minimum temperatures start to increase after mid-winter. Laying when they do means that the chicks hatch in September when the rains start and so have abundant food during the growth phase. However, there must still be sufficient food for the adults to eat during the incubation period, which is probably why the birds in Ndumu bred later than those in Pietermaritzburg in the summers of 1985 and 1986, because there was insufficient food available in Ndumu until September each year. The delay of laying by Lesser Blackwinged Plovers in Ndumu in 1986 indicates that food supply was too low (Chapter 2 - Fig. 2.6) to sustain the parents during incubating; this was shown when some birds came to Ndumu but did not breed at all.

Literature on the lengths of incubation periods of these plovers reveals large differences in incubation period, e.g. Crowned Plovers have been recorded to incubate for 26-29 days (Van der Merwe 1973) and 28-32 days (Maclean 1985), Blackwinged Plovers have been recorded to have incubation periods of 25-26 days (Maclean 1985), at least 26 days (Butcher 1984, MS) and 27-31 days (SAFRING records), while Lesser Blackwinged Plovers have been recorded to have an incubation period of 18-20 days, but probably up to 27 days (Maclean 1985). Although it is possible that incubation period is an adaptive feature of reproduction in these plovers (i.e. the incubation period is shortened if food supplies to the female are good during the egg-development stage allowing her to produce eggs of higher quality which develop faster, or *vice versa*), I would agree with Heim (1974) that it is more likely that constant weather conditions during incubation lead to shorter periods necessary for embryonic development. This remains to be tested experimentally.

Crowned Plovers laid significantly smaller eggs than did Blackwinged Plovers (see Chapter 5) despite the fact that these two species are the same size (Appendix). The small eggs laid by Crowned Plovers do not disadvantage them since the period of vulnerability of the young (from egg-laying to fledging of young) is the same in these two species even though the chick of the Blackwinged Plover is larger at hatching.

Crowned Plovers were the only one of the three species to lay replacement clutches. An extreme case was found by Hanley (1987) in which a pair of Crowned Plovers laid six clutches in a year, two of which survived to hatching but were subsequently lost. The four other clutches were robbed. This, together with their increased degree of iteroparity, indicates why this species is so abundant and widespread in comparison with the other two species.

Incubation

a) *Crowned Plover*

Crowned Plovers display an ability to control brood-patch temperature, although they do not always do so (e.g. pair at Scottsville, Pietermaritzburg). The difference in the incubation behaviour, and resultant nest-air and brood-patch temperatures, of Crowned Plovers at Ndumu and Pietermaritzburg, indicates the amount of inter-pair difference that can occur and still allow the embryos to survive. Because the embryo can withstand great temperature fluctuations, the parent, in the presence of a predator, can stay a long distance from the nest and not attract attention to the eggs. In addition, the parents can spend a long time feeding and thus maintain their body reserves even in times of relatively low food supply.

The long periods that this species can spend off the nest without the embryos dying, together with the relatively small amount of time that the male spends incubating, may allow these birds to become polygynous on occasion (as was found in one instance) and as has been recorded in the Vanellinae in *V. chilensis* (Walters & Walters 1980) and *V. vanellus* (Wilson 1967). However, males of all three study species played a role in incubating the eggs, which increased at higher temperatures. Incubation may not be energetically demanding to the male bird (Norton 1972; Maxson & Oring 1980) since he spends less time incubating than the female, but it may severely curtail the male's time budget, which may be the most important factor selecting for monogamy in the Vanellinae.

The raising of the feathers in all three species during hot periods is probably for cutaneous evaporation (birds caught on the nest at these times were damp with perspiration). Lasiewski et al. (1971) determined that cutaneous evaporation accounted for slightly more than 45% of the total evaporative water loss in nine species studied. This loss of water results in the build-up of salts in the body of the animal which are then excreted via the nasal glands. In cold weather, these plovers also raise the feathers but layer them like tiles so that the distal tip of one feather touches the feather beneath it to trap warm air given off as a result of metabolic energy usage.

The glazed, swollen appearance of the eyes of all three species during hot periods may be associated with the functioning of a rete ophthalmicum which has been shown in Columba livia (Kilgore et al. 1971) to keep the brain 0,94-1,03 °C cooler than the rest of the body. This rete system serves to cool the blood supply to the brain by shunting it out to the eye to allow convective cooling to occur as air passes over the eye's surface.

The legs of Crowned and Blackwinged Plovers became redder during incubation, indicating increased blood supply possibly to facilitate cooling. Raising the body off the eggs occurs because the broodpatch becomes too hot and shading of the eggs is more effective as a cooling mechanism (Grant 1982). Shading in all three species stops in wind because the wind breaks up the boundary layer of cool air between the bird and the eggs and blows warm air across the eggs from the warm ground around the nest and thus increases the temperature of the eggs.

Crowned, Blackwinged and Lesser Blackwinged Plovers faced away from the sun at high temperatures, as did Masked Boobies *Sula dactylata* (Bartholomew 1966) and Kentish Plovers *Charadrius alexandrinus* (Kainady & Al-Dabbagh 1976). Howell (1979) suggested that this behaviour occurs so that the evaporative surfaces of the mouth, which are used extensively in panting and gular fluttering, can function more effectively in the shade of the body, because excessive evaporative water loss is prevented. However, a number of other species nesting in hot environments (*e.g.* Heermann's Gulls *Larus heermanni* (Bartholomew & Dawson 1979), Gray Gulls *Larus modestus* (Howell *et al.* 1974), Snowy Plovers *Charadrius alexandrinus* (Purdue 1976)) orientate randomly with respect to the sun, which may indicate that orientation to the sun may not be that important in preventing excessive water loss in all species.

All three study plovers faced into the wind if the sun was directly overhead, otherwise they only orientated themselves relative to the sun. The orientation of their bodies into the wind reduces the surface area facing the wind and probably prevents excessive water loss via the skin. The prevention of water loss via the skin is less important than preventing this loss via the buccal surfaces because less water is lost via the skin (Schmidt-Nielsen *et al.* 1969) and thus these birds orientate themselves primarily with respect to the sun and secondarily with respect to the wind.

The Crowned Plover has a long incubation-bout duration and starts gular fluttering at higher temperatures than the other two species, indicating that it incurs relatively little thermal stress during incubation. Incubation-bout duration is probably related to body size since small animals get hotter more quickly than larger animals because of their greater surface-area-to-volume ratios. This is shown by the mean incubation-bout duration of Lesser Blackwinged Plovers being shorter than that of Crowned and Blackwinged Plovers.

b) Blackwinged Plover

Blackwinged Plovers kept brood-patch temperatures relatively constant regardless of ambient temperature. Maintaining a constant brood-patch temperature represents a great expense of energy, suggesting that this is necessary for the survival of the embryos (which are probably stenothermic, hence the restricted distribution of this species despite the large size of the adults). These birds appear to suffer from heat stress at high temperatures, unlike the other two species, and this is probably why their distribution is restricted to cooler areas.

Male Blackwinged Plovers spent more time incubating than either other study species , which is probably a result of the need to maintain a constant brood-patch temperature. This species has a long incubation-bout duration which is a feature of large body size.

c) Lesser Blackwinged Plovers

Lesser Blackwinged Plovers did not control brood-patch temperatures closely although they did exhibit some control by keeping the temperatures from increasing at the same rate as ambient temperature. This lack of control is an effect of their relatively small size and, consequently, large surface-area-to-volume ratio. Kendeigh (1970) suggested that smaller birds have less feather insulation and thus gain and lose heat more quickly, leaving them with less control over their body temperatures, which compounds the problem of a large surface-area-to-volume ratio.

Lesser Blackwinged Plovers spent less time shading their eggs than did the other two species, but relieved mates more frequently at the nest to keep brood-patch temperatures low. This differs from the pattern of Crowned and Blackwinged Plovers which relieve partners infrequently and shade the eggs more. Both patterns are successful.

Lesser Blackwinged Plovers, unlike the other two species, had wet legs during the heat of the day, indicating that either they have another mechanism for evaporative cooling (*i.e.* they use a greater area for cooling than the other two species) or they just lose far more water than the others, making this loss more evident.

Schönwetter (1967) suggested that round eggs would be more able to withstand extremes of temperature because of their low surface-area-to-volume ratio. Lesser Blackwinged Plovers have the lowest value of the three study species while Blackwinged Plovers have the highest, which is in accordance with Schonwetter's (1967) hypothesis since Lesser Blackwinged Plovers are found in the hottest climate and Blackwinged Plovers are found in the coolest. Also, the only species of Charadrii in southern Africa to lay eggs with a lower K-value are the small, arid-adapted coursers (Table 4.4). However, Hoyt (1976) has contested Schönwetter's (1967) hypothesis because he maintains that the surface area of the egg is a relatively unimportant feature of incubation when compared with nest insulation, microhabitat selection and incubation patterns, especially as pore area, pore density and shell thickness (which determine the respiratory parameters of the egg (Ar _et al._ 1974; Wangensteen _et al._ 1970)) are independent of surface area. Despite Hoyt's protestations, surface-area-to-volume ratio may be an important feature allowing the birds to stay off the nest for longer in the presence of a predator, say, without the embryo dying. Having a low K-value may be important only to birds with small eggs because arid-adapted birds with large eggs do not have lower K-values than those species that are not arid-adapted (Table 4.4).

Table 4.4. K-values (Schönwetter 1967) of eggs of dryland southern African Charadriiformes. Birds are listed in order of decreasing size.

Species	K value
Burhinus capensis	1,36
Vanellus melanopterus	1,42
Vanellus coronatus	1,38
Rhinoptilus cinctus	1,46
Vanellus lugubris	1,30
Rhinoptilus africanus	1,23
Cursorius rufus	1,27
Cursorius temminckii	1,21

Nest defence

Knight & Temple (1986) challenged the traditional view held by Trivers (1972) and Barash (1975) that birds increase the intensity of nest defence as incubation progresses because they stand to lose more because of greater energy input required to that stage. They found that American Robins *Turdus migratorius* and Redwinged Blackbirds *Agelaius phoeniceus* increased their reaction upon seeing the same predators a number of times (*i.e.* they became imprinted on the intruder) and suggested that the increased reaction detected in other studies was a result of this imprinting. This is certainly the case in Crowned and Blackwinged Plovers, but they also change the type of display towards the end of incubation to a more intense display, regardless of how frequently nests are visited. Lesser Blackwinged Plovers do not defend nests at all, unless a predator actually is about to eat the eggs. These birds rely on crypsis to avoid detection of the nests and also call to attract the predator away from the nest and towards them. The intensity of this display does not increase as incubation progresses regardless of how frequently the nest is visited. All three species defended the young vigorously by mobbing attacks and distraction displays regardless of time of day or temperature, indicating increased intensity with increased energetic investment in the offspring.

All three species became more aggressive morning and evening, regardless of stage of incubation, indicating a greater preparedness to expend energy in the cooler periods of the day (see Fig. 4.39). A possible reason for this lies in the observation by Graul (1975) of a Mountain Plover *Charadrius montanus* dying of what appeared to be a heart attack (the pericardial cavity was filled with blood) while performing a distraction display. These displays may be so energetically expensive that they are usually restricted to periods when energy usage to maintain a constant body temperature is at a minimum.

Chick-tending behaviour

The "creche system" adopted by the three study plovers to care for the young is another behaviour that indicates that cooperation is well developed in these plovers and is probably induced by low food availability in the grasslands, which requires a more efficient time budget than is allowed in a usual biparental-care system.

Chick growth

The transition from down to contour feathers edged with buff to maintain the crypticity of the young is in line with the rest of the reproductive strategy of these plovers to cope with the exposure of the eggs and young to predators. This strategy includes having cryptic eggs, the distraction display of the adults, cryptic young and the removal of eggs from the nest. All this has developed as a result of living in exposed habitats where the eggs and young are very vulnerable to predation. The fast growth rate of the chicks is also part of this strategy to get the chicks to fly at an early age, which is similar to the strategy exhibited by other vanelline plovers (Walters 1980; Dann 1981).

Reproductive success

The hatching success of all three study species (except Lesser Blackwinged Plovers in 1986) was considerably higher than the average of 54% ascribed to precocial, groundnesting birds (Lack 1954). This high hatching success is probably attributable to the sophisticated anti-predatory behaviours employed by these species. Blackwinged Plovers had the highest hatching success because of their wariness and ability to detect predators from a long way off (the nests of this species were by far the most difficult to find). The great difference in fledging success of this species obtained from observance of eggs through hatching to flying young and from counting the number of fledged young at Scottsville Racecourse is probably because Blackwinged Plovers did not breed there and may have lost young to predation en route or they may have become separated from them.

The fledging success obtained for Crowned Plovers was higher in this study than the values obtained by Hanley (1987) in the eastern Cape (30,2% over 11 years), a factor which Hanley attributes to high predation by Yellow Mongoose (Cynictis penicillata) there. Predation is certainly the most important factor affecting reproductive success in all three study species and can cause huge differences in reproductive success between two study sites, e.g. of 39 eggs laid by 17 pairs of Crowned Plovers in Ndumu in May/June 1986, only two young survived to flying age. All of the chicks and eggs lost were taken by Pied Crows.

The great change in reproductive success in Lesser Blackwinged Plovers between 1985 and 1986 was in part the result of predation on nests (two out of nine) and partly of desertion (three out of nine) possibly caused by low food availability to the incubating adults; the latter possibility is supported by the fact that many birds initiated breeding behaviour but did not breed.

Chapter 5

ALLOMETRY AND THE BREEDING BIOLOGY OF SOME PLOVERS

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ABSTRACT

Some of the variables previously considered to be adaptive features of the life histories of animals in r/K-selection theory (MacArthur & Wilson 1967) have been shown to be an effect of body size (Millar 1977, Western 1979). Body size was found to affect egg size, offspring size at hatching, incubation period, incubation ability and, consequently, mating system in Crowned Plovers *Vanellus coronatus*, Blackwinged Plovers *V. melanopterus*, Blacksmith Plovers *V. armatus* and Lesser Blackwinged Plovers *V. lugubris*. Clutch size was the key adaptive variable of reproduction in Lesser Blackwinged Plovers, while degree of iteroparity was the key adaptive variable in the life-history of Crowned and Blacksmith Plovers. Blackwinged Plovers showed no

variation in any reproductive variable.

ALLOMETRY AND THE BREEDING BIOLOGY OF SOME PLOVERS

INTRODUCTION

Some animals produce few large young (*e.g.* most of the larger higher vertebrates) and others produce many small young (*e.g.* many invertebrates). These life-history patterns are often summarized in terms of *r* and *K* selection theory (MacArthur & Wilson 1967). In the case of *r*-selection, a population is kept at a low density by some external agent (*e.g.* weather or predation) and only rarely approaches the carrying capacity of the environment in which it lives. Under such conditions, individuals with a high reproductive output should be at a selective advantage because they would be able to exploit favourable circumstances, when they arise. A *K*-selected population, on the other hand, is near the carrying capacity of its environment and competitive interactions between individuals are expected to be important in population regulation. Selection in this case should therefore favour individuals with high competitive ability rather than high reproductive output. Animals described as *K*-strategists are generally associated with relatively stable environments.

Variations of these life-history patterns occur, however, even within species. For example, clutch sizes of temperate-zone birds are often larger (and are thus more *r*-selected) than those tropical-zone members of the same species (Owen 1977). In addition, Nichols *et al.* (1976) have shown that numerous organisms inhabiting variable environments exhibit temporally dynamic reproductive patterns. Populations of such organisms demonstrate considerable variation in reproductive effort associated with environmental changes and therefore shift between relative *r* and *K* positions on an *r*-*K* continuum.

In considering the features affecting the life-histories of animals and the variations in the reproductive pattern adopted by a species, many theorists have not considered the capacity of an animal to alter its reproductive output. Numerous studies have been done, usually on mammals, to determine the extent of the scaling relationships between metabolic rate (as approximated by body weight) and various life-history variables (Millar 1977, Western 1979). This has led to the epigenetic concept of life-history patterns, which ascribes differences in life-history variables to scaling relationships rather than reproductive adaptations to environmental features, as is the case with *r/K* selection theories. Scaling relationships of the following life-history features to metabolic rate (as approximated by body weight) have been demonstrated: gestation length (Kihlstrom (1972), lifespan (Sacher 1959), birth rate (Western 1979), net reproductive rate (Western 1979), age at first reproduction (Western 1979), intrinsic rate of natural increase (Fenchel 1974), total weight of newborn young (Leitch *et al.* 1959) and postnatal growth (Millar 1977).

Millar (1977) suggested that, since relative offspring size is a conservative feature of reproduction in many mammalian orders, litter size is the key adaptive variable of reproduction. Perrin (1985), however, suggested that litter size might be the key adaptive variable for what he termed "energy bet-hedgers", while degree of iteroparity is the key adaptive variable of reproduction for "temporal bet-hedgers". Energy bet-hedgers have a short period available to them when food supply is optimal for breeding. They vary the energy commitment to breeding (depending on the food supply available before breeding) by altering litter size. Temporal bet-hedgers have a long period available to them during which food supply is optimal for breeding. During seasons of high resource availability, they capitalize by increasing their degree of iteroparity. Litter size in these animals appears to be fixed. Perrin (1985) suggested that his theory allows for the compatibility of *r/K* selection and bet-hedging theories.

Birds of the order Charadriiformes are suitable species in which to examine many of the theories outlined above, since they appear to be temporal bet-hedgers (*sensu* Perrin 1985) and are typical *K*-selected animals, producing few, large, precocial young. Members of this order typically have a modal clutch size of four (Maclean 1972, Winkler & Walters 1983). The distribution of clutch size is truncated, very few birds laying more than four eggs (*e.g.*

Blacksmith Plover *Vanellus armatus* - Fig. 1). Is the small, truncated clutch size of charadriiform birds a result of body size, or is *K*-selection acting ? Can these birds hedge their bets and change their reproductive patterns depending on environmental conditions ? Do egg-formation ability, incubation ability or predation control clutch size ?

Charadriiform birds exhibit the greatest variety of mating systems shown in the class Aves, including monogamy, polygyny, polyandry and lek-mating (Johnsgard 1981). Individual male or female birds may increase their reproductive outputs by being polygynous or polyandrous respectively. Therefore, the adoption of a polygamous breeding system may be a way in which members of this order can alter their reproductive outputs, within the limitations of a small clutch size.

Crowned Plovers *Vanellus coronatus*, Blackwinged Plovers *V. melanopterus* and Lesser Blackwinged Plovers *V. lugubris* were examined in this study because they are closely related and two of these species are of a similar size (Crowned and Blackwinged Plovers, both with a mean weight of 167 g), while the Lesser Blackwinged Plover is smaller (mean body weight of 117 g), so the effect of body size on life history can be studied. In addition, all three species occupy similar habitats, namely short, open grasslands, although Lesser Blackwinged Plovers usually nest in open woodlands. All three species are monogamous.

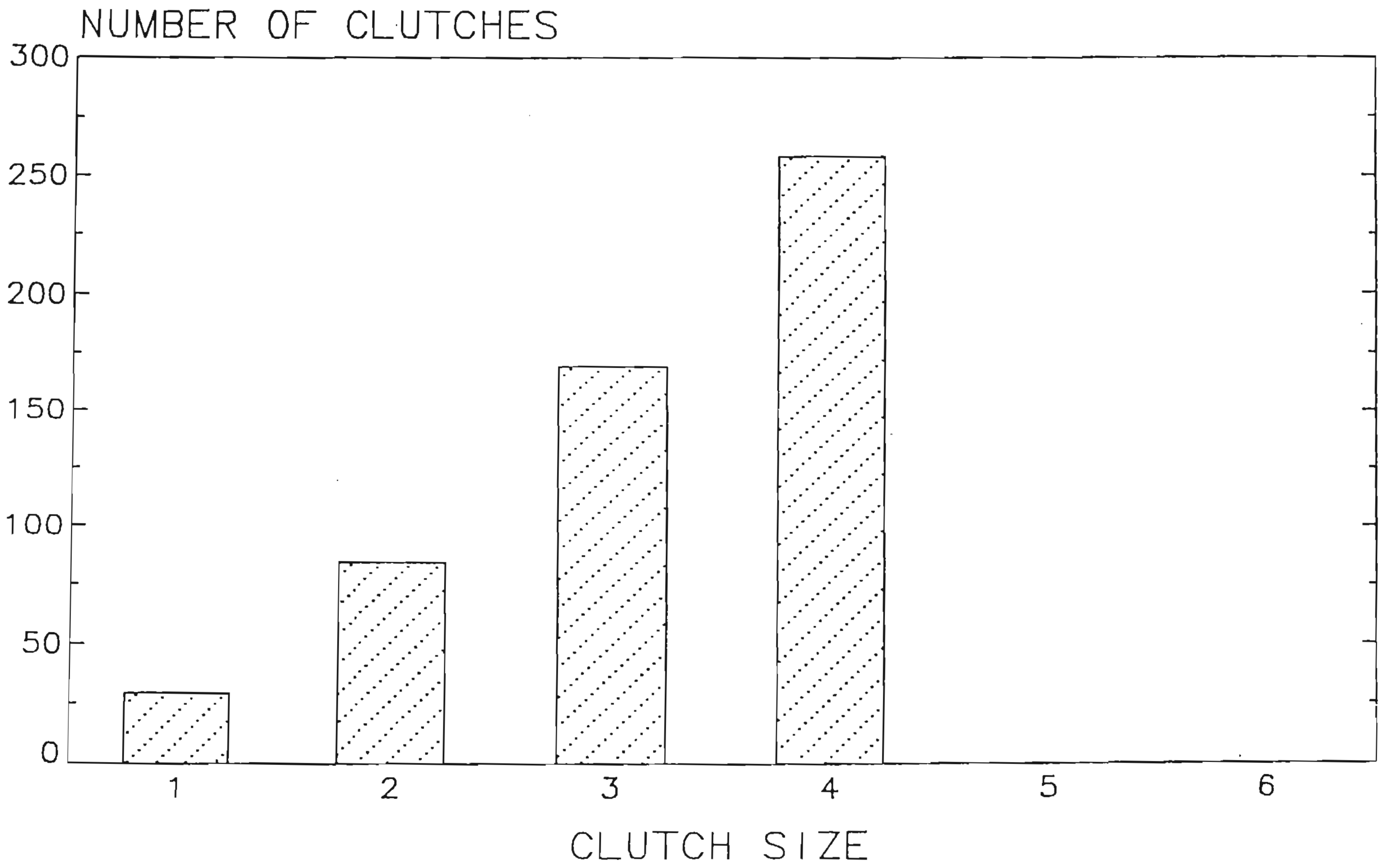


Fig. 1. Clutch size of Blacksmith Plover in southern Africa.

MATERIALS AND METHODS

Crowned and Blackwinged Plovers were studied in the vicinity of Pietermaritzburg, South Africa, while Lesser Blackwinged and Crowned Plovers were studied in the vicinity of Ndumu, northern Natal, South Africa, from January 1985 until June 1987. Data were obtained from 57 clutches of Crowned Plovers, 18 clutches of Blackwinged Plovers and 31 clutches of Lesser Blackwinged Plovers. Egg volumes were computed by measuring the length and greatest breadth of each egg with vernier calipers and inserting these values into Hoyt's (1979) formula $\underline{V} = \underline{L.B}^2$. Data on egg measurements of southern African Charadriidae were obtained from Maclean (1985). Additional data on clutch size were obtained from the Southern African Bird-ringing Unit (SAFRING) at the University of Cape Town, South Africa. Because plovers lay one egg per day (Johnsgard 1981), only clutches that were visited on more than four separate days were accepted for analysis, in order to ensure that only complete clutches were considered.

Two eggs were added to each of two 3-egg Crowned Plover clutches and two 4-egg Lesser Blackwinged Plover clutches to test whether these birds were able to incubate more than four eggs.

The incubatory behaviour of four pairs of Crowned Plovers, three pairs of Blackwinged Plovers and three pairs of Lesser Blackwinged Plovers were studied for the duration of their respective incubation periods.

Arthropod availability to these insectivorous birds was determined by counting the numbers of arthropods in a 0.25 m^2 quadrat, which was thrown to the ground every 5 m along a 100-m transect through the birds' feeding areas.

RESULTS

Any changes in reproductive output may come about in one or more of the following three stages: egg-laying, incubation and post-hatching stages.

Egg-laying stage

The egg volumes of members of the southern African Charadriidae show a strong positive correlation with mean adult female body weight (Fig. 2). However, Crowned Plovers laid significantly smaller eggs than did Blackwinged Plovers ($t_{49.3} = 7.35$, $p < 0.001$), although these two species are the same size. The length of the incubation period is positively correlated with egg size in 15 members of the genus _Vanellus_ for which information is available (Johnsgard 1981)($\underline{r}^2 = 0.58$; $p < 0.01$). Incubation period is also positively correlated with adult-female body weight ($\underline{r}^2 = 0.57$; $p < 0.01$). A linear regression of adult female body weight and egg size to length of the incubation period

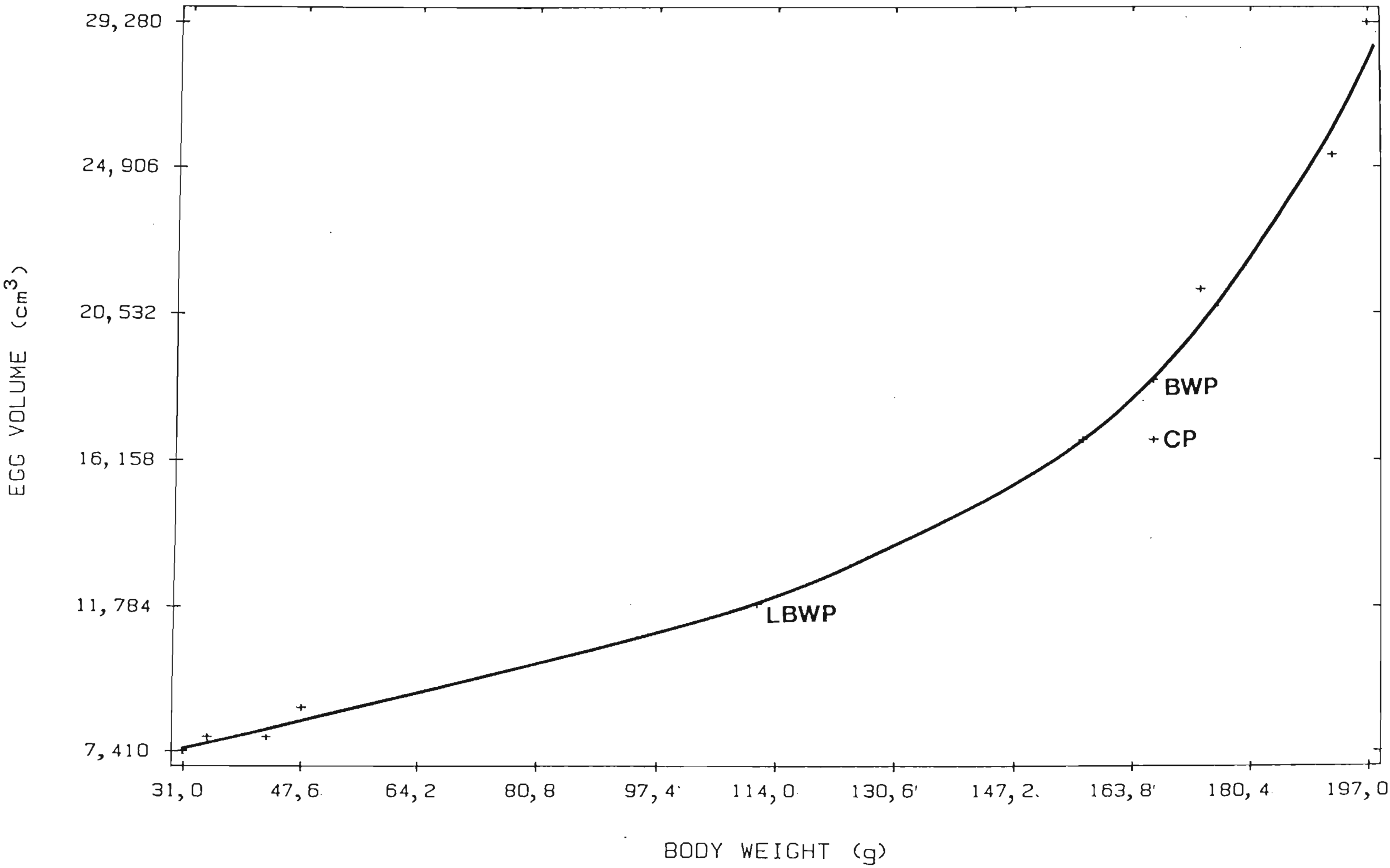
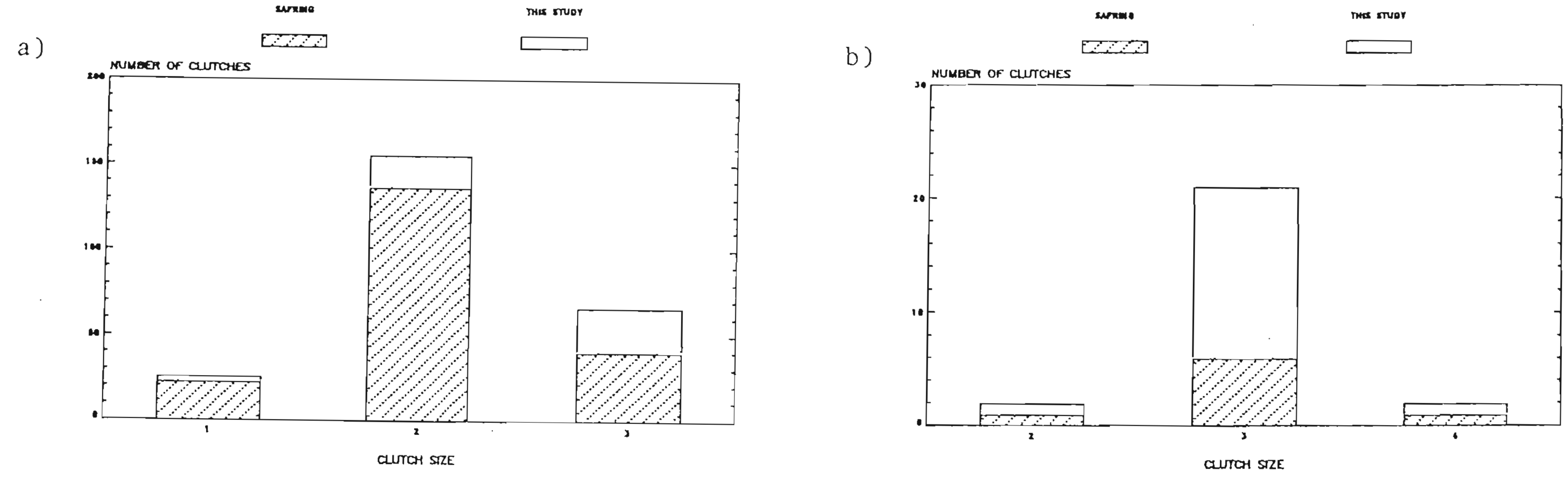


Fig. 2. Relationship between egg volume and female body weight in members of the southern African Charadriidae. Best-fit curve is $y = 1/(0.15 - 0.001x)$; $\underline{r}^2 = 0.99$; $p < 0.001$. CP = Crowned Plover; BWP = Blackwinged Plover; LBWP = Lesser Blackwinged Plover.

yields the following equation : Incubation period = 19.2 + 0.064.body weight - 0.177.egg volume ($r^2 = 0.60$; $p < 0.01$).

Crowned, Blackwinged and Lesser Blackwinged Plovers laid smaller clutches than the modal clutch size for the order (Figs 3a, b and c). There was no significant change in egg size with different clutch sizes in Crowned Plovers (clutch size 1 vs 2: $t_5 = 0.32$, $p > 0.05$; clutch 1 vs 3 : $t_{23} = 0.26$, $p > 0.05$; clutch size 2 vs 3: $t_{56.1} = 0.14$, $p > 0.05$) and Lesser Blackwinged Plovers (clutch size 3 vs 4: $t_{26.5} = 1.04$, $p > 0.05$). There were insufficient 2-egg clutches of Lesser Blackwinged Plover to compare with clutches of three and four eggs. Since only one 2-egg and one 4-egg clutch of Blackwinged Plovers were found, no comparisons were made for this species.

There was no significant difference between the clutch volumes (egg volume x clutch size) of Crowned and Lesser Blackwinged Plovers ($t_{48.1} = 1.81$, $p > 0.05$), whereas clutch volumes of Blackwinged Plover were significantly larger than those of either of the other two species (Blackwinged Plover vs Crowned Plover: $t_{49.3} = 7.35$, $p < 0.001$; Blackwinged Plover vs Lesser Blackwinged Plover: $t_{40.1} = 4.23$, $p < 0.001$). If mean clutch volume is divided by mean adult-female body weight, then Lesser Blackwinged Plovers had the highest reproductive output (0.40 cm^3/g body weight), followed by Blackwinged Plovers (0.33 cm^3/g body weight) and then Crowned Plovers (0.23cm^3/g body weight). There was no significant difference in clutch size in Crowned and Blackwinged



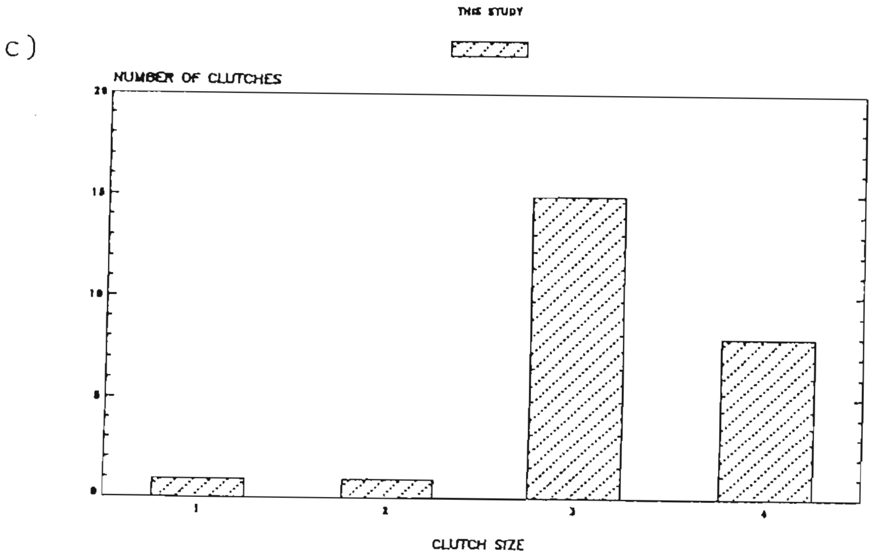


Fig. 3. Clutch sizes of: (a) Crowned Plover - $\bar{x}$ $\underline{+}$S.E. = 2.09 $\underline{+}$0.04, (b) Blackwinged Plover - $\bar{x}$ $\underline{+}$S.E. = 3.00 $\underline{+}$0.06, (c) Lesser Blackwinged Plover - $\bar{x}$ $\underline{+}$S.E. = 3.20 $\underline{+}$0.14.

Plovers between clutches laid in 1985 and 1986 ($p > 0.05$), although Lesser Blackwinged Plovers laid significantly smaller clutches in September-October 1986 (which was a dry year - Fig. 4) than in September-October 1985 ($t_{29} = 2.77$, $p < 0.01$).

Crowned Plovers may breed in every month of the year (Fig. 5), although in this study, clutches were recorded only in August-October 1985 and August-October 1986 in Pietermaritzburg and in September-October 1985, May-June 1986, September-October 1986 and May 1987 in Ndumu. It appears that Crowned Plovers usually lay clutches before the onset of spring rains in September, but if there is a sudden increase in food availability at any other time of year they will breed. This was certainly the case in May-June 1986 at Ndumu Estates (3 km south of Ndumu Game Reserve), where there was a sudden emergence of Harvester Termites <u>Hodotermes mossambicus</u>. The mean number ±S.E. of arthropods per quadrat in Ndumu Game Reserve (where Crowned Plovers were present but did not breed) was 2.08 ±0.85 compared with 14.06 ±1.21 termites per quadrat at Ndumu Estates. Food availability was not measured during the unseasonal breeding of Crowned Plovers in May-June 1987. Blackwinged and Lesser Blackwinged Plovers did not breed unseasonally and have only been recorded breeding from July-October and August-November, respectively (pers. obs., SAFRING records).

Only Crowned Plovers at Ndumu had two broods in a year (n = 5 pairs of marked birds). Six pairs of Crowned Plovers laid

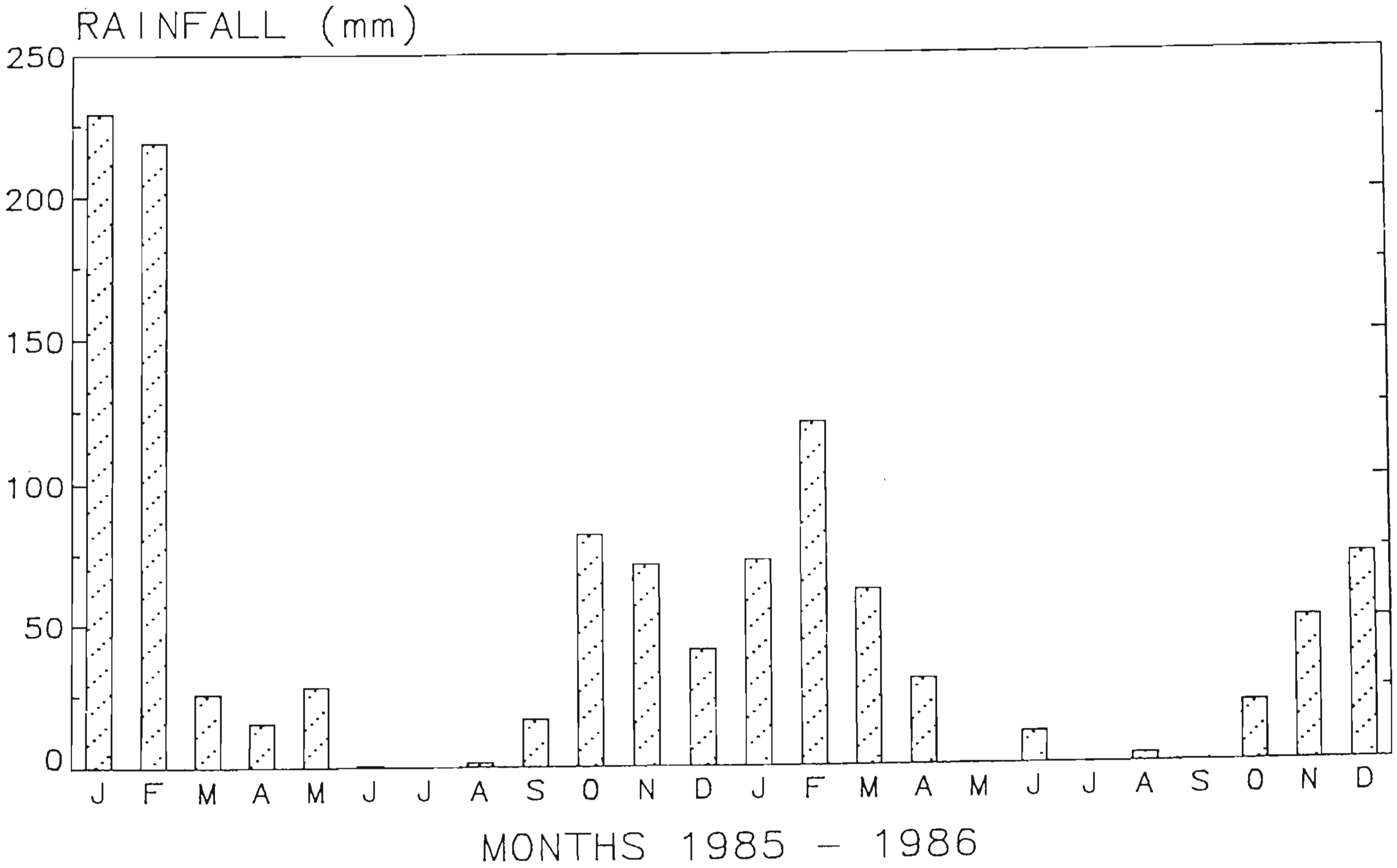


Fig. 4. Rainfall at Ndumu in Ndumu in 1985 and 1986.

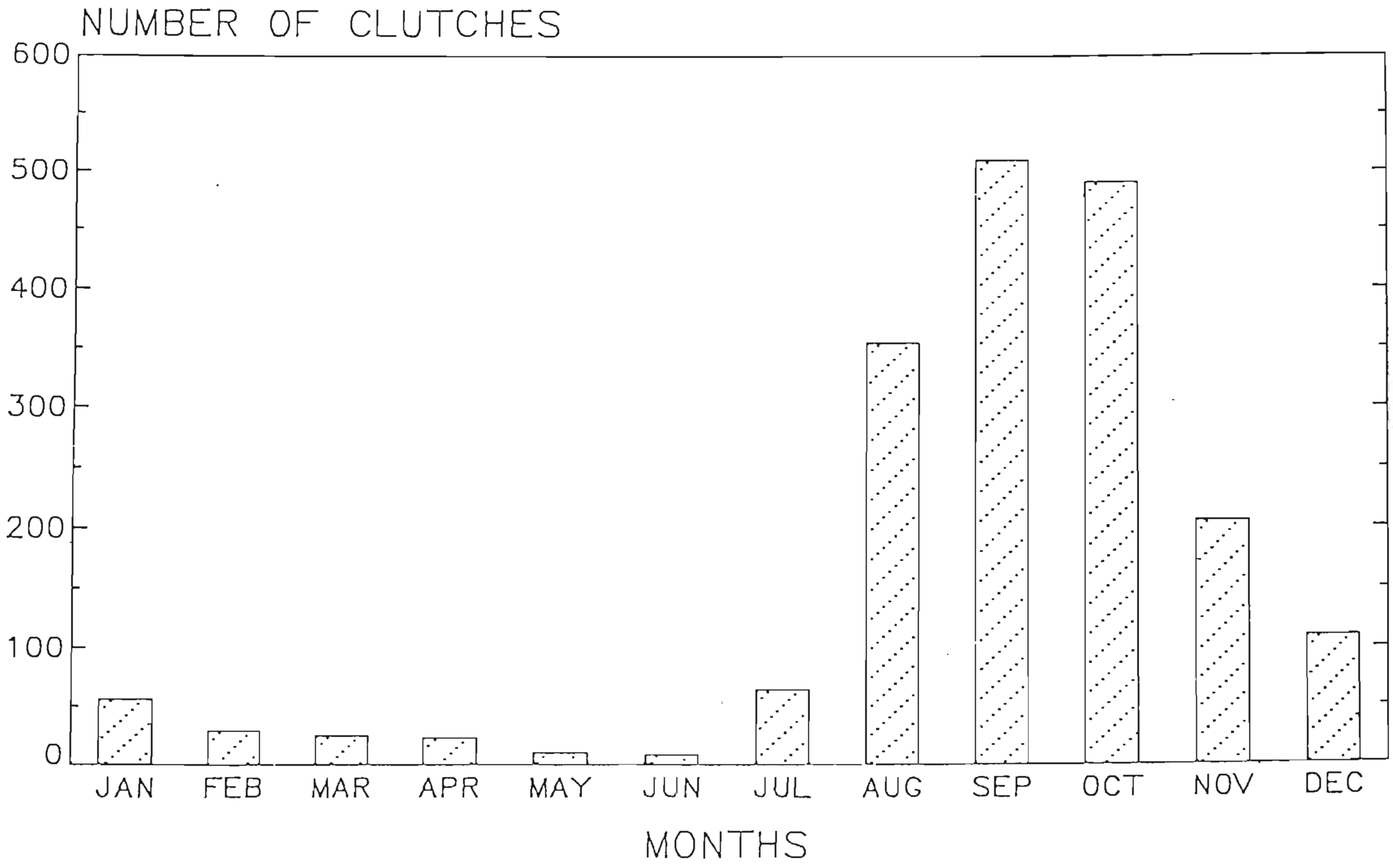


Fig. 5. Time of egg-laying of Crowned Plover in southern Africa.

replacement clutches within a week of losing their first clutches. Neither Blackwinged nor Lesser Blackwinged Plovers laid replacement clutches or had two broods in a year.

Blacksmith Plovers also had two broods in a year in Pietermaritzburg and Ndumu (n = 4 pairs of marked birds). This species has also been recorded breeding in every month of the year (Fig. 6).

Incubation stage

Male Crowned, Blackwinged and Lesser Blackwinged Plovers assisted the females of their respective species in the incubation of eggs, increasing their time on the nest at temperatures above 40°C (all three species), and at temperatures below 20°C (Blackwinged Plovers). Male Crowned Plovers incubated for 27.9% of the time (n = 472.4 h) during which nests of this species were observed, male Blackwinged Plovers did 37.9% of incubation (n = 152.9 h), while male Lesser Blackwinged Plovers did 40.4% of incubation (n = 170.7 h).

Incubation-bout duration (i.e. length of time that a bird incubated before being relieved by other parent) of Crowned and Blackwinged Plovers was significantly longer (mean ±S.E. = 92.60 ±7.10 min and 92.79 ±10.71 min respectively) than Lesser Blackwinged Plovers (mean ±S.E. = 40.12 ±4.15min). There was a significant decrease in incubation-bout duration of Lesser

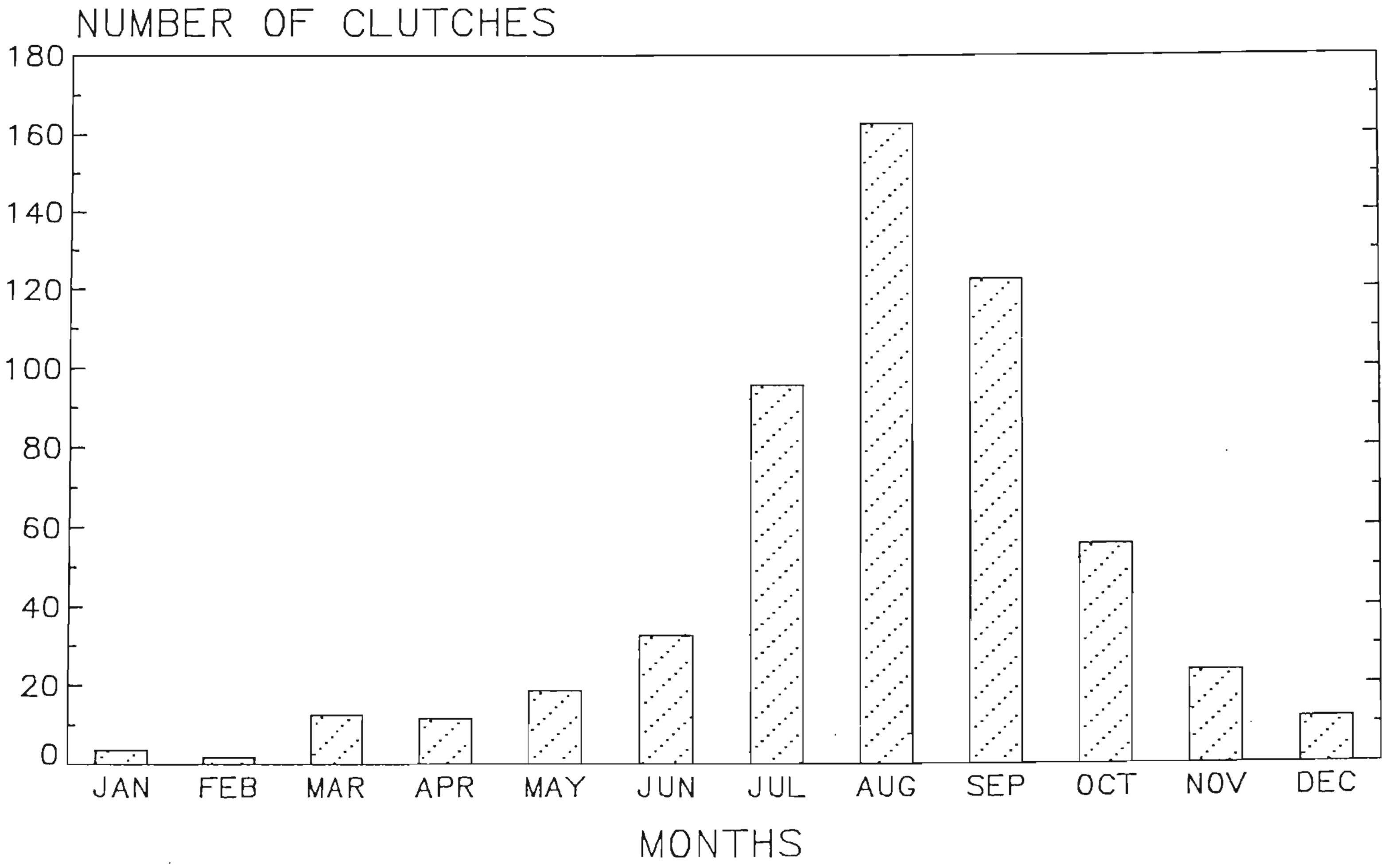


Fig. 6. Time of egg-laying of Blacksmith Plover in southern Africa.

Blackwinged Plovers at higher temperatures ($p < 0.05$), while there was no significant change in incubation-bout duration of either Crowned or Blackwinged Plovers over the range of temperatures measured ($p > 0.05$).

All the eggs in the augmented broods of Crowned and Lesser Blackwinged Plovers hatched.

Post-hatching stage

Crowned, Blackwinged and Lesser Blackwinged Plovers actively tended their young by showing them food. Male and female parents took turns to care for the young. Territories were not maintained by any of these species during this stage. Blacksmith Plovers did not actively tend the young, leaving them to search for food themselves. Blacksmith Plovers maintained permanent territories.

DISCUSSION

The strong positive correlation of egg size with female body weight in the South African Charadriidae, as well as the positive correlation of egg size and adult body weight with incubation period, indicate that egg size (and, consequently, offspring size at hatching), as well as embryonic growth rate, are not adaptive features of reproduction in these species. This contradicts r/K-selection theory, which suggests that selection for offspring size occurs as a response to either environmental disturbance (*r*-selection) or environmental stability (*K*-selection). The apparent lack of ability to alter offspring size at hatching is supported by the lack of change in egg size with change in clutch size.

Crowned Plovers laid significantly smaller eggs than did Blackwinged Plovers, which suggests that they expend less energy in egg production in order to achieve some pay-off in another aspect of their reproductive output. Crowned Plovers were the only species to have two broods in a year and appear to be the only species of the three that ever does so, according to SAFRING records, although records of clutches are meagre for Blackwinged and Lesser Blackwinged Plovers. It would appear then that Crowned Plovers lay smaller eggs but can increase their degree of iteroparity if a sudden emergence of arthropods occurs. Therefore, Crowned Plovers have a higher output in terms of egg volume per unit body weight than the other two species if they do breed twice a year, despite having the lowest clutch volume per unit body weight of the three species.

The ability to form eggs does not appear to limit clutch size, at least in Crowned Plovers, because some birds of this species do lay replacement clutches if their clutches are taken by predators or if they desert their first clutches because of disturbance.

The requirement that males share incubation with the females because the females get too hot during long spells on the nest is probably the most important factor necessitating monogamy in these three species. The ability to control body temperature at high ambient temperatures is greater in Crowned and Blackwinged Plovers than in Lesser Blackwinged Plovers, presumably because smaller birds have a larger surface-area-to-volume ratio than larger birds and consequently gain heat more quickly. The relative difficulty which small birds experience in controlling their brood-patch temperatures in hot climates is probably the most important factor in the evolution of greater size in the genus *Vanellus*, which has an African centre of origin (Bock 1958), and has evolved from a basal stock within the genus *Charadrius* (Strauch 1978) which has its centre of origin in the temperate Holarctic (Bock 1958).

Crowned and Lesser Blackwinged Plovers were able to incubate clutches that were larger than the modal four eggs usual for the Charadriiformes, which indicates that incubatory ability is not a limiting factor on clutch size in these species.

Safriel (1975) hypothesized that a clutch of four eggs was modal for the Charadriiformes because this was the optimal clutch size resulting from minimizing the visibility of the brood to predators and maximizing reproductive output. Why then do Crowned, Blackwinged and Lesser Blackwinged Plovers lay smaller clutches than is usual for the order ? Walters (1982) suggested that a large amount of energy was required to tend precocial chicks despite the hypothesis of Lack (1968) that only altricial young require a high energy input from the parents. Walters suggested that inactive tenders (a group which includes the waterside vanelline plovers such as Blacksmith Plovers and Longtoed Plovers _V. crassirostris_ (Walters 1982)) do not lead their young to food because they maintain territories year-round and cannot afford to attract attention to the young within this limited space. These inactive tenders all have modal clutches of four eggs because they do not have to divide their time and energy between feeding themselves and their young. Inactive tenders may also have a higher mortality at the chick stage than active tenders because chicks have to find their own food (and thus might starve due to lack of experience in finding food) and parents are not as capable as active tenders are of warning the chicks about the presence of predators because of the distance between parents and chicks. High chick mortality may, therefore, be an important factor selecting for larger clutch size in inactive tenders than in active tenders. Active tenders are usually grassland species which do not maintain territories on account of the continual growth of grass until it becomes too tall for the plovers, forcing these birds to move to more suitable habitats. Active tenders, such as Crowned, Blackwinged and Lesser Blackwinged Plovers, expend a lot of time and/or energy showing food to the young. Since they deprive themselves of time to feed, they have smaller clutches than inactive tenders in order to improve the chances of all the young (as well as the parents) surviving the tending period. In addition, a reduced clutch is necessary to decrease the conspicuousness of the brood to predators because the presence of the parents close to the young while actively tending them makes the brood more conspicuous than inactively tended young.

CONCLUSIONS

The small clutch size of Crowned, Blackwinged and Lesser Blackwinged Plovers appears to be limited by the active tending of young, which would place larger broods at greater risk of predation in the exposed habitats in which these birds live.

Body size has an important effect on the life-history styles of Crowned, Blackwinged and Lesser Blackwinged Plovers, affecting size of offspring at hatching, incubation period and incubation ability and, consequently, mating system.

The two variables of reproduction appear to be, as Perrin (1985) suggested, degree of iteroparity (Crowned and Blacksmith Plovers) and clutch size (Lesser Blackwinged Plover).

It appears, then, that body size must be taken into account when studying the life-history adaptations of animals. The study of life-history adaptations of animals to specific environmental conditions, as is suggested by r/K-selection theory, should consider only those parameters that deviate from an allometric scaling to body weight.

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Chapter 6

SYSTEMATIC RELATIONSHIPS

INTRODUCTION

The relationships between the species of the family Charadriidae, and in particular members of the Vanellinae, have been debated since the work of Seebohm (1888). Subsequent workers have proposed a number of classifications (Peters 1934; Bock 1958; Strauch 1978) which have either split the species into a large number of genera, often monotypic (Peters), or lumped them into a few genera (Bock), both classifications being considered equally unsatisfactory (Johnsgard 1981).

As a result, Crowned, Blackwinged and Lesser Blackwinged Plovers have been variously classified into the genera *Stephanibyx* (Peters 1934) and *Vanellus* (Bock 1958). Blackwinged and Lesser Blackwinged Plovers have been considered to constitute a superspecies by Snow (1978) and Johnsgard (1981) on account of plumage similarities. However, numerous behavioural differences were found to occur between these two species while Crowned and Blackwinged Plovers were found to be behaviourally similar, leading to an attempt at re-examining the relationships between species as postulated by previous workers.

Bock (1958) suggested that the most effective means of determining relationships between birds of the family Charadriidae would be by the use of biochemical and behavioural characters, as a result of his inability to detect differences between species on the basis of skeletal characters.

For these reasons it was decided that a behavioural comparison be made of Crowned, Blackwinged and Lesser Blackwinged Plovers to determine their phylogenetic relationships. In addition, the behaviour of Blacksmith and Wattled Plovers was compared with the three above-mentioned species to determine the meaning of various behaviour patterns and to determine which behavioural characters are of value in a systematic study and which characters are not phylogenetically useful.

A comparison was also made of various skeletal characters of the above-mentioned birds in order to test whether the relationships indicated by behavioural characters were congruent with phylogenies proposed by analysis of morphological characters.

MATERIALS AND METHODS

The behaviour of Crowned, Blackwinged, Lesser Blackwinged, Wattled and Blacksmith Plovers was observed in the field and recorded in a notebook. In addition, the reaction of all five species to playback of their own and the other four species' vocalizations was noted.

Qualitative features of five skeletal specimens of Wattled Plovers and Blacksmith Plovers were examined. Skeletons of eleven Crowned Plovers, seven Blackwinged Plovers and six Lesser Blackwinged Plovers were also examined. Skeletal features were compared with descriptions provided by Strauch (1978) in his analysis of the relationships between members of the order Charadriiformes. Five Crowned, Blackwinged, Lesser Blackwinged, Blacksmith and Wattled Plover syringes were examined by longitudinal sectioning in 7 μm sections, set in wax and stained with Mallory's stain (Grimstone & Skaer 1972) for 4 min. Five eggshells of each of Crowned, Blackwinged, Lesser Blackwinged, Wattled and Blacksmith Plovers were examined under a scanning electron microscope to compare pore structure.

Analyses of the relationships between species (= Operational Taxonomic Units or O.T.U.s) were performed using an unweighted pair group method using arithmetic averaging (UPGMA) on a SPSS programme. This method was employed with both the City Block (or Manhattan) metric and squared Euclidean distances to determine the difference between O.T.U.s based on a correlation matrix. The correlation matrix was derived using the Pearson product-moment correlation coefficient to determine the correlation between the variables of each O.T.U. A weighted-pair cluster analysis (WPGMA) was performed using a SIGSTAT programme. This technique clusters pairs of O.T.U.s based on a correlation matrix and weights the O.T.U. most recently admitted to a cluster equal with all previous members. The Euclidean distance measure was used to determine the difference between O.T.U.s in the WPGMA analysis. Prim networks (Prim 1957) were also used to display differences between O.T.U.s.

RESULTS

Behaviour

The following behavioural displays were noted and differences compared for the five vanelline plover species:

a) Post-copulatory wing-lifting display: as the male bird dismounts after copulation, he stands behind the female and lifts both wings to a vertical position (Wattled Plover), or the male stands alongside the female and each bird lifts the wing further from the other bird to a vertical position (Crowned Plover), or the behaviour found in Crowned Plovers is altered by the display being performed while both birds run for about 1 m (Blackwinged Plover). Neither Lesser Blackwinged Plovers nor Blacksmith Plovers performed a post-copulatory wing-lifting display.

b) Butterfly-flight display: used by male plovers to demonstrate territorial ownership and to attract females. This display involves flying above the territory in a circular path with exaggerated wingbeats, emphasizing the down-stroke and making a short, quick up-stroke. This display occurred in Crowned, Blackwinged, Blacksmith and Wattled Plovers. Lesser Blackwinged Plovers performed a display using a circular flight-path but did not use a butterfly-flight pattern.

c) Nest-scrape display: precedes copulation and involves one bird (male) lying down about 1 m behind the other (female), both birds' chests touching the ground, and then followed by kicking out backwards with their feet. Only Blacksmith Plovers performed this display.

d) Double-wing flick agonistic display: when threatened or when threatening conspecifics, other bird species or predators, Crowned, Blackwinged, Wattled and Blacksmith Plovers lift both wings vertically to display the contrasting black-and-white coloration of the wings. This display is concurrent with a small jump (5 cm high), although in cases of extreme conspecific interaction a bird may jump over another bird while performing this display. Lesser Blackwinged Plover juveniles also performed this display when threatened, although adults rarely did. Only a slight jump occurred in Lesser Blackwinged Plovers concurrent with this display. Lesser Blackwinged Plovers never performed this display in conspecific encounters.

e) Bobbing threat display: when threatened by terrestrial predators or other plovers, the initial reaction of all five vanelline plover species was to bob the entire body backwards while keeping the legs motionless. Lesser Blackwinged Plovers, however, frequently bobbed their heads up-and-down in a single, quick movement in the manner of members of the genus <u>Charadrius</u> (pers. obs.).

f) Intraspecific anxiety display: when entering a territory occupied by conspecifics or a conspecific-roosting area, all five vanelline plover species displayed anxiety by flicking their tails sideways.

g) Interspecific anxiety display: when confronted by a allospecific plover or a potential terrestrial predator, all five plover species flicked their tails downwards in an anxiety display.

h) High-intensity intraspecific threat display: the head was held low and the neck feathers ruffled as the bird (all five plover species) chased off intruders. Lesser Blackwinged Plovers also kicked out backwards with their feet, one foot at a time, brushing up loose soil.

i) Interspecific threat display: in cases of attack by terrestrial predators, all vanelline plovers except Lesser Blackwinged Plovers spread their wings horizontally and lowered their heads as they approached the intruders. This display was followed by aerial mobbing. Lesser Blackwinged Plovers, however, spread their wings horizontally but did not lower their heads while performing this display. They did not perform an aerial-mobbing display except when they had chicks less than two weeks old.

j) Nest- and chick-defence displays: during the first 20 days of incubation, Crowned, Blackwinged, Wattled and Blacksmith Plovers aerially mobbed intruders. After this period, aerial mobbing was performed in addition to a "broken-wing display" (Crowned and Blackwinged Plovers only) which involved lying with the chest on the ground with wings horizontally outstretched so that the wings touched the ground. The wings were flapped up and down, with the tips never lifting more than about 5 cm from the ground. All five species also crouched down and, with the wings held closed, vigorously flapped the wings close to the body. Lesser Blackwinged Plovers did not perform the "broken-wing display" but did stand upright, with the head held erect, and flapped both wings forward in front of the body in a "clapping" motion.

The differences in behaviour between the species are summarized in Table 6.1.

Crowned, Blackwinged, Wattled and Blacksmith Plovers all responded to playback of one another's calls by threat displays and displacement activities (such as feeding, copulation and false-brooding). These four species did not respond to Lesser Blackwinged Plover calls and Lesser Blackwinged Plovers did not respond to their calls. Lesser Blackwinged Plovers responded to playback of their own calls by threat displays and displacement activities mentioned above.

The phenetic relationships between the species using behavioural characters are represented in a Prim network (Fig. 6.1 a).

Morphology

The differences in syrinx morphology between the five species are documented in Table 6.2. These differences were not considered significant enough to use as systematic characters until more

Table 6.1. Differences in behaviour of Crowned, Blackwinged, Lesser Blackwinged, Wattled and Blacksmith Plovers.

Species	Behaviour pattern						
	a	b	c	d	e	f	g
Crowned Plover	2	1	2	2	1	2	1
Blackwinged Plover	2	1	2	2	1	2	1
Lesser Blackwinged Plover	1	1	1	1	1	1	2
Blacksmith Plover	2	1	1	2	2	2	1
Wattled Plover	2	2	1	2	1	2	1

a = presence (2) or absence (1) of a double wing-flick display

b = presence (2) or absence (1) of a post-copulatory display employing 2 wings

c = presence (2) or absence (1) of post-copulatory display employing 1 wing

d = presence (2) or absence (1) of an inverted U-note in territorial call

e = presence (2) or absence (1) of a nest-scrape display

f = presence (2) or absence (1) of butterfly flight display

g = broken-wing display performed while standing upright (2) or with belly on ground (1)

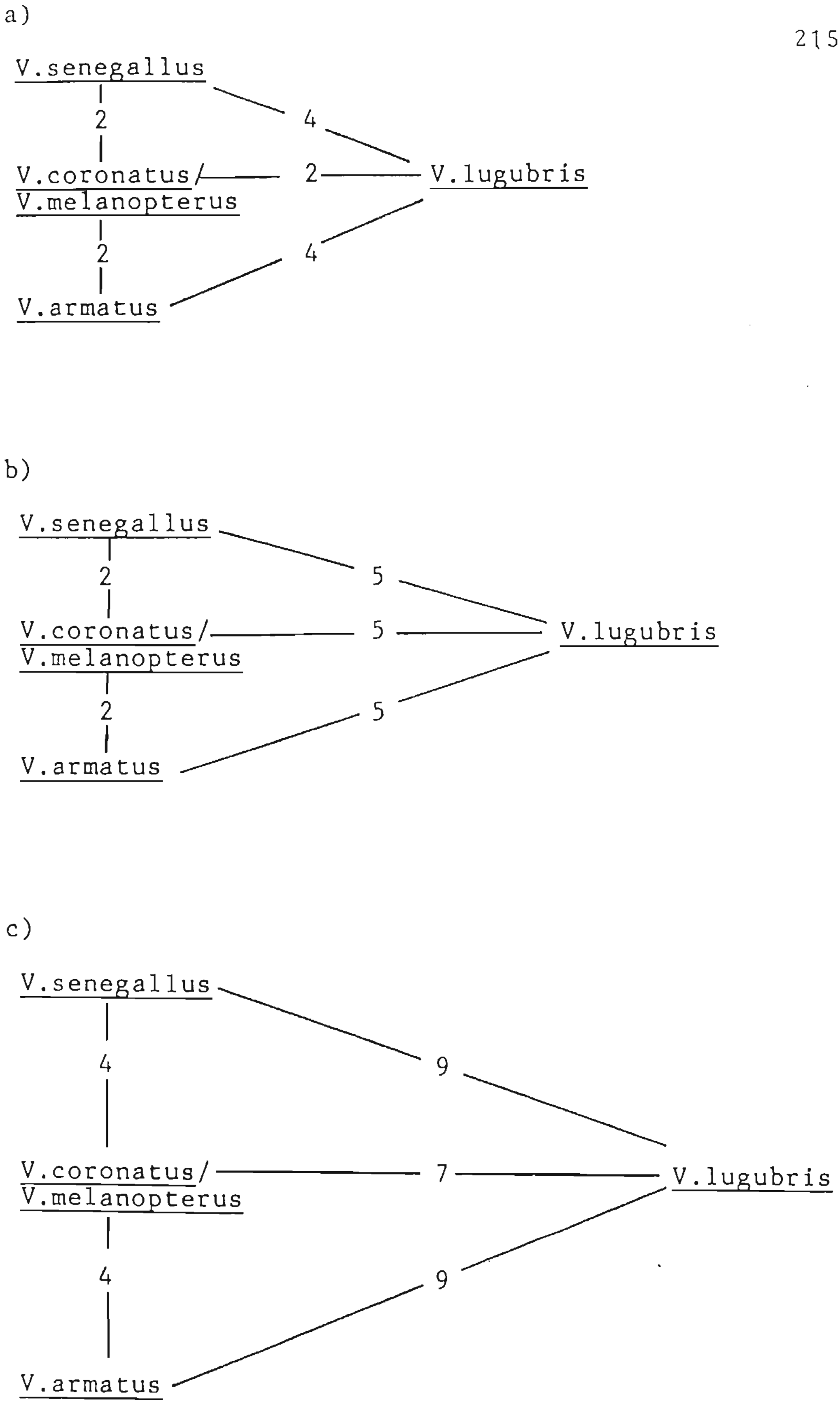


Fig. 6.1. Prim networks showing the differences between Crowned, Blackwinged, Lesser Blackwinged, Wattled and Blacksmith Plovers. Numbers indicate the number of characters that differ between the species joined by the lines. (a) behavioural characters

Table 6.2. Differences in syrinx morphology between Crowned, Blackwinged, Lesser Blackwinged, Wattled and Blacksmith Plovers.

Species	Tracheal rings	Bronchial rings	Pessulus
Crowned Plover	Fibrocartilage	Fibrocartilage	Fibrocartilage
Blackwinged Plover	Fibrocartilage	Fibrocartilage	Fibrocartilage
Lesser Blackwinged Plover	Fibrocartilage	Cartilage	Cartilage
Blacksmith Plover	Fibrocartilage	Fibrocartilage	Fibrocartilage
Wattled Plover	Bone	Fibrocartilage	Fibrocartilage

syringes of member-species of the genus Vanellus are examined to determine whether the differing degrees of ossification are important or are merely correlated with body- or syrinx-size. A generalized Vanellus syrinx, based on the structure of the syringes of the five species examined, is shown in Fig. 6.2.

The pores of Lesser Blackwinged Plover eggs were the largest of all the species examined while those of Crowned and Blackwinged Plovers were the smallest (Fig. 6.3a, b, c, d and e).

The members of the genus Vanellus are separated from other members of the Charadriidae by the presence of an additional cervical vertebral strut. In the cluster analysis of the skeletal features of members of the Vanellinae several characters used by Strauch (1978) were omitted because they were found to be either incorrectly classified or variable within a species. A maxillopalatine strut (strut C sensu Strauch) was not included in the analysis as Strauch recorded it as absent in Lesser Blackwinged Plovers when it was found to be present in all specimens of this species examined in this study. Thus, it is possible that this character was incorrectly coded for other species too. The number of supraoccipital foramina was excluded because this character was variable in all the species examined, being present in young specimens and absent in larger, older birds. These foramina are presumed to ossify with age. The shape of the posterior-medial edge of the ilium was also excluded from the analysis because it was found to be variable within all the

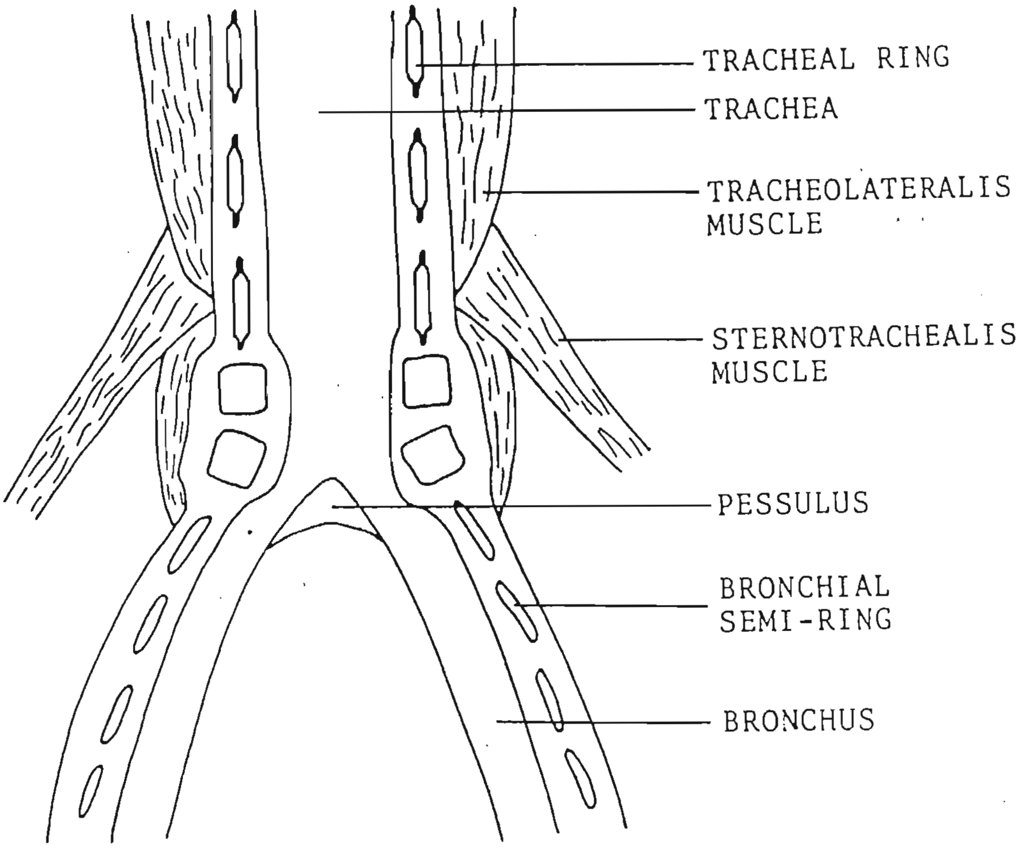
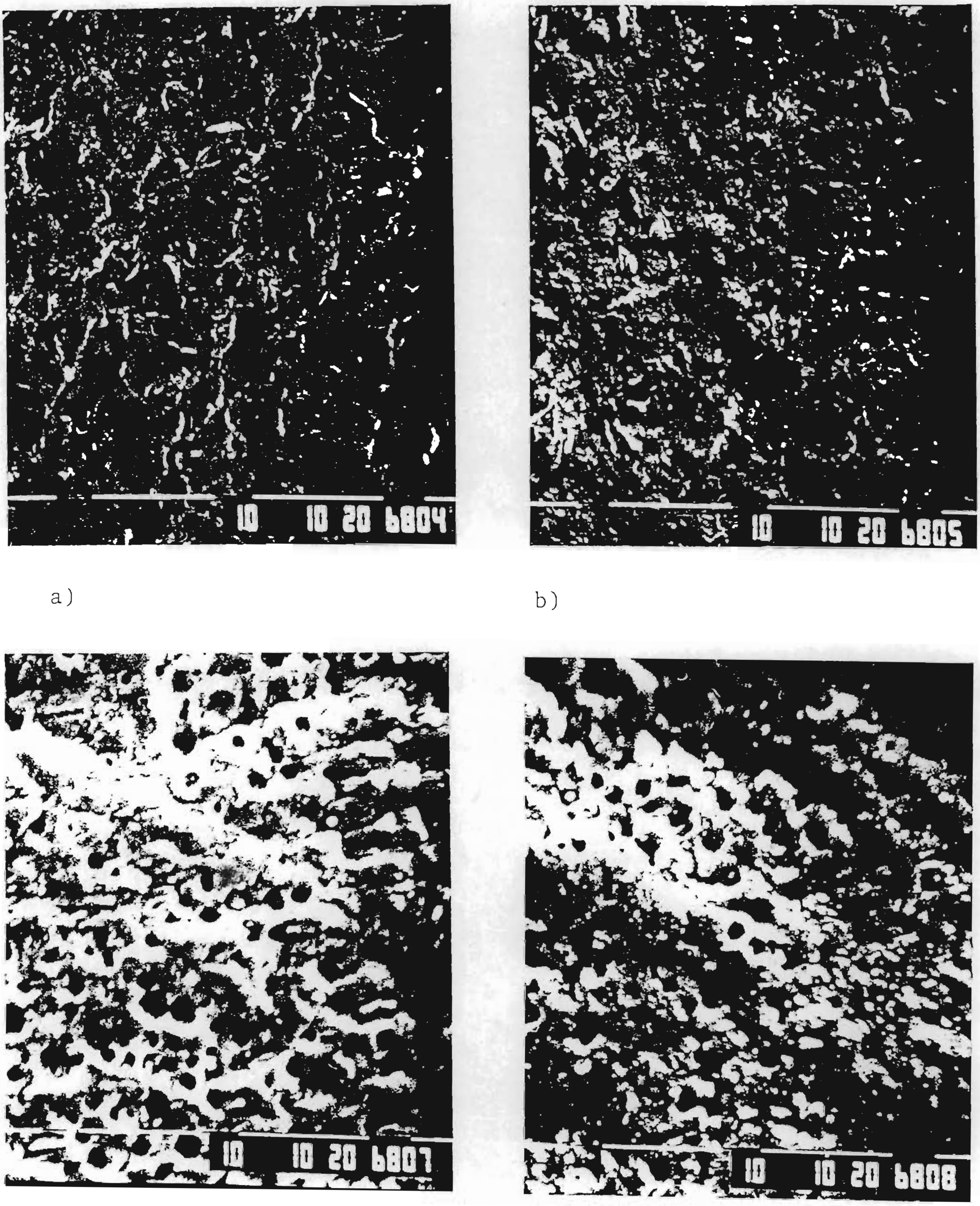


Fig. 6.2. A generalized Vanellus syrinx based on the structure of Crowned, Blackwinged, Lesser Blackwinged, Wattled and Blacksmith Plover syringes.



a) b)

c) d)

Fig. 6.3. Pore structure of Crowned (a), Blackwinged (b), Blacksmith (c and Wattled Plover (d) eggshells viewed under scanning electro microscope. Magnification = 2000X.

e)

Fig. 6.3e. Pore structure of Lesser Blackwinged Plover eggshell viewed under scanning electron microscope. Magnification = 2000X.

species examined.

The following features were used in the morphological analysis; (a) the number of caudal vertebrae, omitting the pygostyle, (b) the number of cervical vertebrae, omitting those with unfused cervical ribs, (c) presence or absence of a wing spur, (d) presence or absence of a hallux, (e-g) presence or absence of canals in the hypotarsus for tendon numbers 4, 5 and 6 (*sensu* Strauch 1978), (h) presence or absence of a red iris, (i) black-tipped or white secondary feathers, (j) tail white or with a black band in it, (k) presence or absence of wattles.

A further 60 skeletal characters were examined (these were the other characters used by Strauch (1978)) and found to be invariable between the *Vanellus* species examined and were therefore not included in the analysis. All characters mentioned by Strauch (1978) for species not examined in this study were taken as being correct, with the exception of the characters mentioned above as being variable within species or incorrect for the species examined. The presence of red eye-colour and the two plumage features were included in the analysis because they are considered to be synapomorphic because they are not present in other members of the Charadriidae. All other plumage characters examined were found to be symplesiomorphies and thus excluded from the analysis. The differences between the skeletal features of the Charadriidae studied are shown in Table 6.3.

Table 6.3. Differences in morphological characters of the members of the genus *Vanellus*. Species with the same number share the same state of a character.

	a	b	c	d	e	f	g	h	i	j	k
V.malabaricus	1	1	1	2	1	1	1	1	1	1	2
V.melanopterus	1	1	1	2	1	1	1	1	1	1	1
V.lugubris	1	1	1	2	2	1	1	1	2	1	1
V.tricolor	2	2	1	2	1	1	1	1	1	1	2
V.gregarius	1	1	1	1	1	1	1	1	2	1	1
V.leucurus	1	2	1	1	1	1	1	2	2	2	1
V.coronatus	1	1	1	2	1	1	1	1	1	1	1
V.cinereus	1	1	1	1	1	1	1	2	2	1	2
V.tectus	2	1	1	2	1	1	1	1	1	1	2
V.vanellus	2	2	1	1	1	1	1	1	1	1	1
V.chilensis	2	2	2	1	1	1	1	2	1	1	1
V.resplendens	2	2	2	2	1	1	1	2	1	1	1
V.albiceps	1	2	2	2	1	1	1	1	2	1	2
V.senegallus	1	1	2	1	1	1	1	1	1	1	2
V.spinosus	1	1	2	2	1	1	1	2	1	1	1
V.armatus	1	1	2	2	1	1	1	2	1	1	1
V.duvaucelii	2	1	2	2	1	1	1	2	1	1	1
V.miles	2	1	2	1	1	2	1	1	1	1	2
V.macropterus	1	1	2	1	1	2	1	1	1	1	2
V.indicus	1	1	2	1	1	2	1	2	1	1	2
V.crassirostris	2	1	2	1	1	2	2	2	1	1	1

a = Seven (1) or eight (2) caudal vertebrae, omitting the pygostyle

b = 12 (2) or 13 (1) cervical vertebrae, omitting those with unfused cervical ribs

c = presence (2) or absence (1) of a wing spur

d = presence (1) or absence (2) of a hallux

e = presence (1) or absence (2) of a hypotarsal canal 4

f = presence (2) or absence (1) of a hypotarsal canal 6

g = presence (2) or absence (1) of a hypotarsal canal 5

h = presence (2) or absence (1) of a red iris

i = black-tipped (1) or white (2) secondary feathers

j = tail white (2) or with black band in it (1)

k = presence (2) or absence (1) of wattles.

A Prim network of the relationships between Crowned, Blackwinged, Lesser Blackwinged, Wattled and Blacksmith Plovers using morphological characters is presented in Fig. 6.1b. A Prim network (Fig. 6.1c) displays the number of characters that differ between species using behavioural and morphological characters. The results of the cluster analyses of morphological characters of all members of the genus *Vanellus* except *V. melanocephalus* and *V. superciliosus* are presented in Figs 6.4, 6.5 and 6.6.

DISCUSSION

The use of behavioural characters for phylogenetic analysis has been disputed by Mayr (1970) on account of these features being adaptive and subject to change independent of phylogenetic change. However, while this can not be disputed, behavioural characters, together with external morphology, calls and pheromones, are the constituents of a species' mate recognition system, which delineates one species from another (Paterson 1980). As long as one uses behavioural characters which are not adaptive they are as valid a taxonomic character as any other in that they convey information of characters developed during the phylogeny of that organism.

The debate continues as to whether cladistic or phenetic methodology is more accurate in the determination of the phylogeny of an organism (Hennig 1966; Sneath & Sokal 1973; Wiley 1981; Sokal 1985). Phenetic methodology potentially suffers from

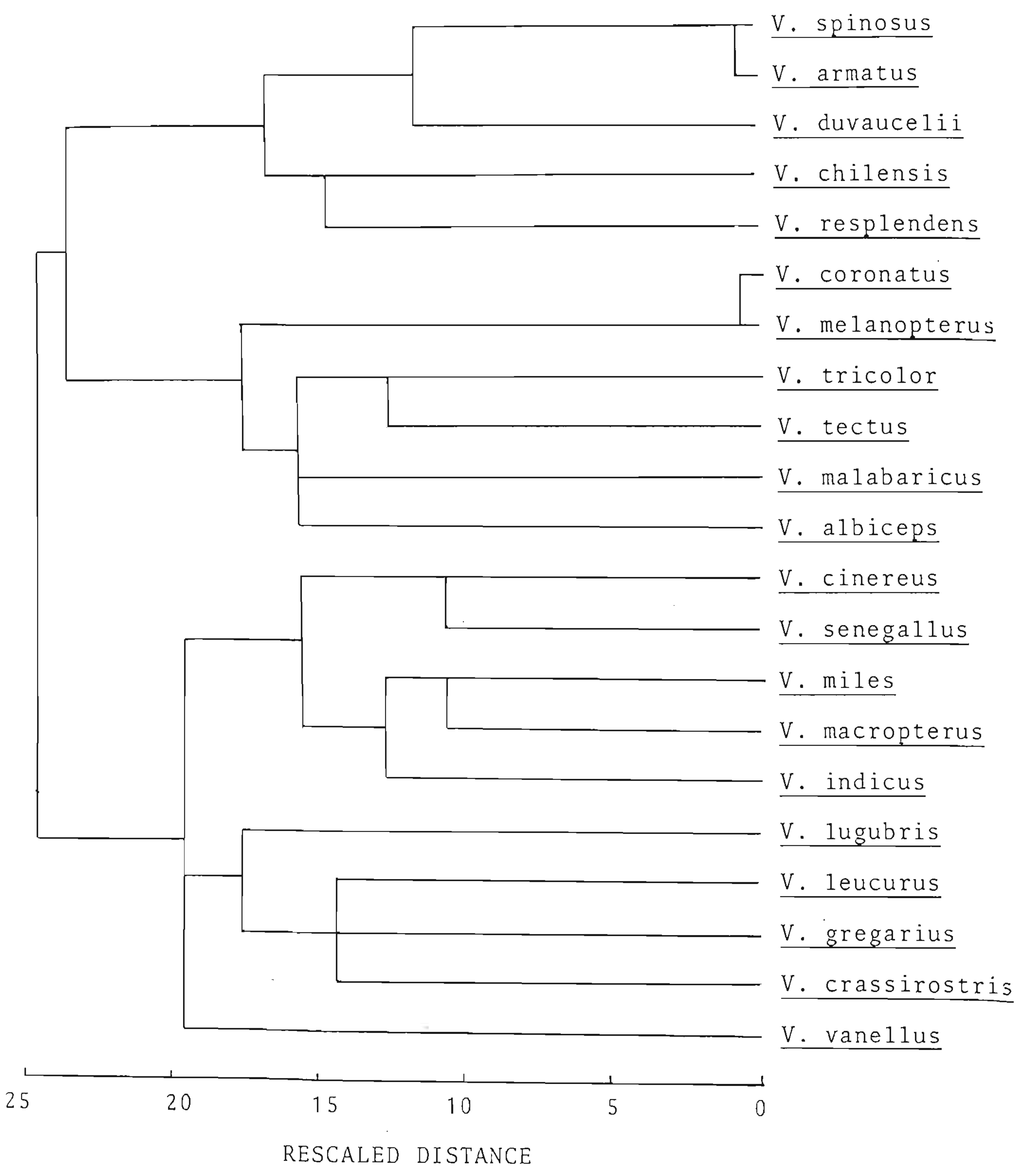


Fig. 6.4. Phenogram derived by unweighted-pair cluster analysis (UPGMA) using the city block distance measure on a correlation matrix on morphological characters of species of *Vanellus*.

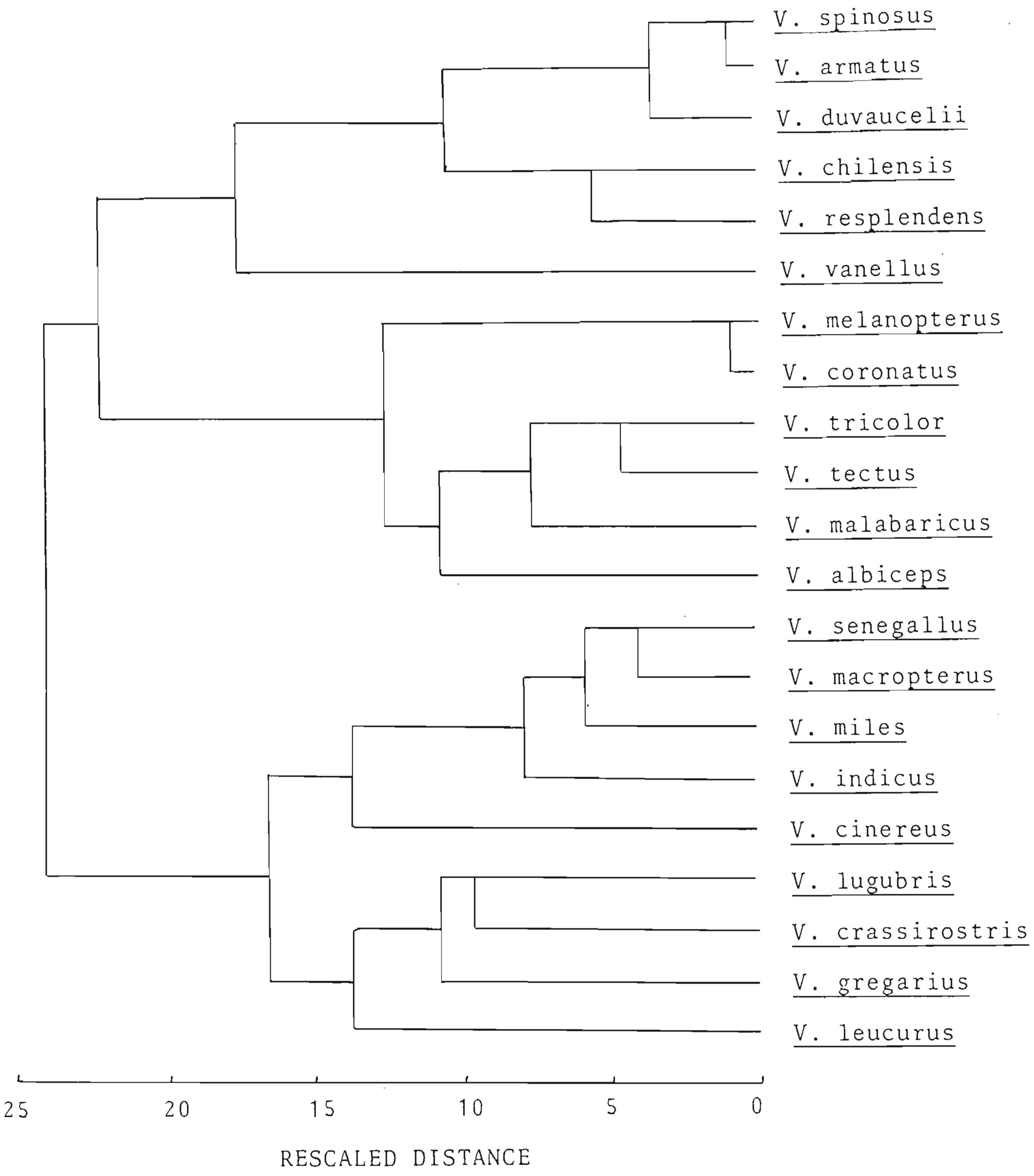


Fig. 6.5. Phenogram derived by unweighted-pair cluster analysis (UPGMA) using the squared Euclidean distance measure on a correlation matrix on morphological characters of species of *Vanellus*.

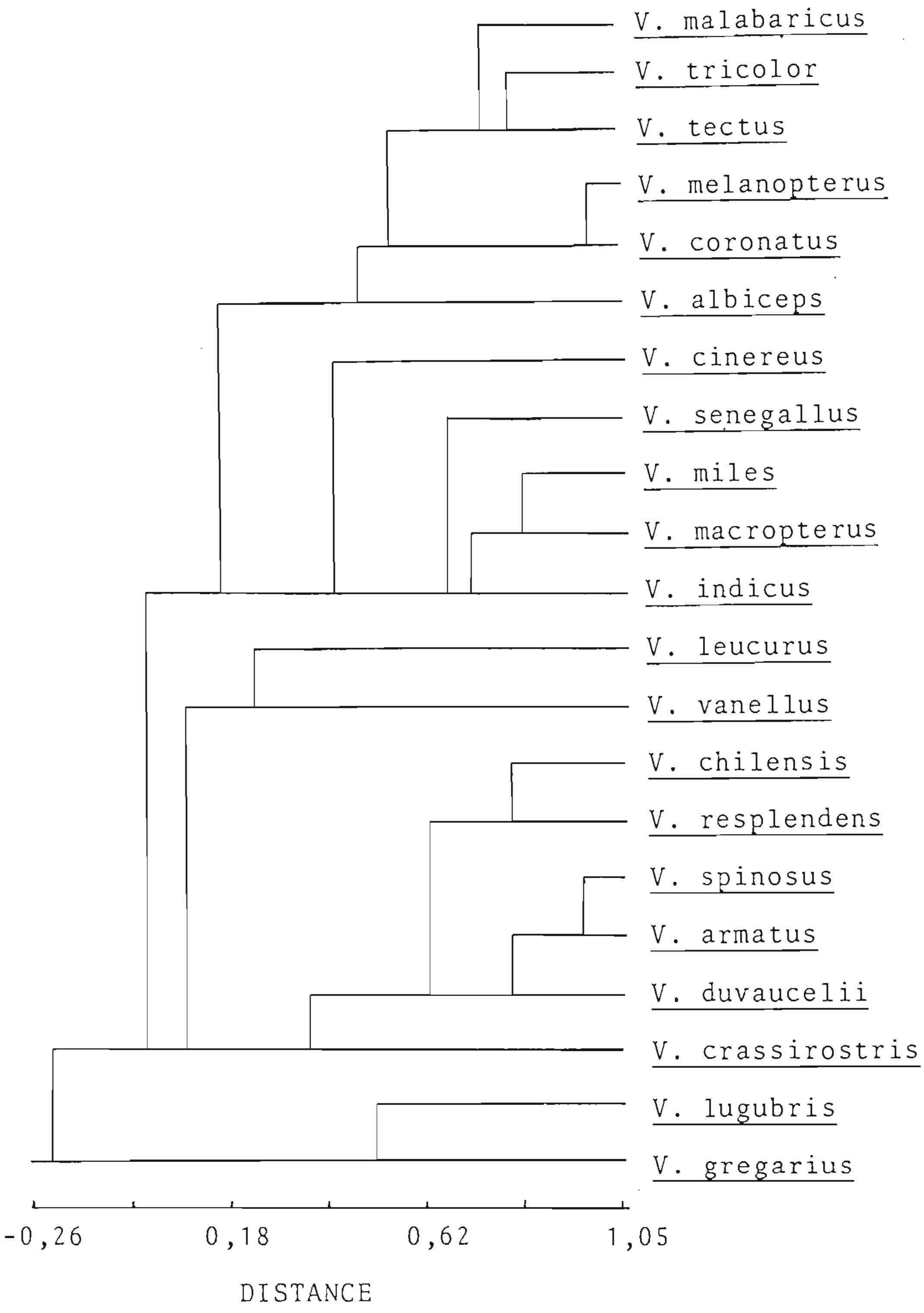


Fig. 6.6. Phenogram derived by weighted-pair cluster analysis (WPGMA) using the Euclidean distance measure on a correlation matrix on morphological characters of species of *Vanellus*.

the use of characters that are not of phylogenetic importance swamping phylogenetic characters because of the number of non-phylogenetic characters used in the analysis. Cladistics requires decisions as to the primitive and derived states of characters, which have to be made on the basis of comparison with the states of these characters in groups of species which are assumed to be closely related to the group in question. I have used the phenetic method because it is considered to be more accurate than cladistics when few characters are used (Sokal 1985).

The pore structure of Lesser Blackwinged Plover eggshells deviates from the trend shown by Board (1982) that arid-adapted birds have smaller eggshell pores than waterside birds in order to reduce water loss from the egg. The other plover species' eggs examined in this study lend support to Board's (1982) findings because the waterside species (Blacksmith and Wattled Plovers) have large eggshell pores while the grassland species (Crowned and Blackwinged Plovers) have small eggshell pores. The biological significance of the unusual eggshell structure of Lesser Blackwinged Plovers is not known.

The Prim networks using behavioural and morphological characters and behavioural as well as morphological characters and the phenograms using morphological characters all demonstrate that Blackwinged and Crowned Plovers are more similar to one another than to any other <u>Vanellus</u> species. In addition, Lesser

Blackwinged Plovers are not as similar to Blackwinged Plovers as general plumage characters would appear to suggest. On the basis of this initial analysis I suggest that Blackwinged and Lesser Blackwinged Plovers do not constitute a superspecies as has been suggested by Snow (1978) and Johnsgard (1981) but that Crowned and Blackwinged Plovers constitute a superspecies group. The lack of stereotyping of certain *Vanellus* behaviour patterns in the Lesser Blackwinged Plover (bob and double-wing flick) and the absence of the butterfly-flight display indicate that this species has not diverged much from the ancestral stock of this genus. The similarity of plumage of Blackwinged and Lesser Blackwinged Plovers may be the result of lack of change from an ancestral plumage which is displayed in members of the genus *Charadrius* (*e.g.* Whitefronted Plover *C. marginatus* and Kentish Plover *C. alexandrinus*), a group from which *Vanellus* is probably derived (Strauch 1978).

The phenograms of the morphological relationships of members of the genus *Vanellus* do not all produce the same result but they all cluster Crowned and Blackwinged Plovers together and show them to be distinct from Lesser Blackwinged Plovers. These analyses agree with my hypothesis, based on behavioural characters, that Crowned and Blackwinged Plovers are very similar and possibly constitute a superspecies.

This analysis must remain tentative until the behaviour of the other *Vanellus* species has been adequately described, in order to broaden the basis of selection of behavioural characters for systematic analysis. By demonstrating which characters have been used, this systematic analysis can be re-examined by other workers using other techniques and by supplementing these characters with others to develop, ultimately, a more rigorous analysis which will more accurately reflect the true phylogeny of the genus *Vanellus*.

EPILOGUE

Much of this study has involved a natural-historical approach to the biology of Crowned, Blackwinged and Lesser Blackwinged Plovers. In the framework of the "Popperphilia" prevalent in biology today (Diamond 1986) which promotes hypothetico-deductivism and experimental falsifiability (Popper 1963), descriptive biology appears to have little value in providing new insights. However, several biologists have rallied to support the role of natural history in biology (e.g. Colwell 1984; Diamond 1986; Bartholomew 1986), mostly from the point of view that it is is not always feasible to manipulate animals in their natural surroundings. According to Bartholomew (1986), systematic observation and judicious use of deduction and inference can allow naturalists to work effectively from organismal to ecosystem levels. Colwell (1984) suggested that "realistic experiments with primate or bird communities are not very much more feasible than experiments in astrophysics, but our curiosity about stars and starlings [read 'planets and plovers'] is not thereby lessened." The natural-history study of Crowned, Blackwinged and Lesser Blackwinged Plovers has been necessary, I believe, to allow the establishment of hypotheses that are potentially falsifiable and the progression of scientific study of these organisms.

The feeding ecology of Crowned and Blackwinged Plovers in an area of syntopy indicated that interspecific competition was not an important factor in the relationship between the two species, and that the two species coexist, in spite of apparently diffuse competition for food, in order to detect predators more easily and to spend more time feeding. This is yet another study that demonstrates the need for a "paradigm shift" (Kuhn 1970) in community-ecology theory away from the school of thought that interspecific competition dominates the relationships between species using the same resources, because of the opportunistic nature of these and many other animals and the importance of other factors such as predation and environmental disturbance.

However, despite the plethora of scientists demonstrating the lack of importance of interspecific competition (e.g. Connell 1980; Price 1980; Walter et al. 1984; Den Boer 1985) this theory persists as dogma. I fear, as Kuhn (1970) did regarding scientific paradigms in general, that "paradigm shifts do not come about because proponents of earlier paradigms agree that the new hypothesis is shown to greatly improve one's interpretation of the science, but rather, that old scientists die". Since many of the proponents of competition theory are in their 50s and 60s and have managed to convince their students of the apparent value of this paradigm, we may have a long time to wait for this paradigm shift.

I suggest that a new paradigm should centre around a view which encompasses a philosophy of biology in general that individuals are the unit of natural selection and that populations evolve.

Species, according to this view, are merely groups of individuals from separate populations (except in those cases where a species occurs as one population) which can potentially interact genetically with one another to affect the evolution of the population. This view recognizes interspecific competition (or, rather, interpopulation competition) as being important in affecting populations in the short and long term, but emphasizes that competition is only one of a multitude of factors (which include predation, food availability and environmental disturbance) that mould interpopulation relations and, ultimately, evolution.

The breeding biology of Crowned, Blackwinged, and Lesser Blackwinged Plovers emphasizes the importance of size in the biology of organisms. The relatively poor ability of small birds, such as the Lesser Blackwinged Plover, to regulate their body temperatures while incubating because of their large surface-area-to-volume ratios indicates that studies of the smaller Charadrius plovers and coursers (Cursoriinae) incubating in arid environments would prove a useful line of research in order to determine the minimum size that a bird may be in an arid environment, incubating in an exposed site. These results should also be supported by experiments in a laboratory with all environmental conditions being manipulated.

The results of experiments conducted on clutch size indicate that Safriel's (1975) hypothesis that predation is a limiting factor on clutch size may be valid. This theory should be tested by examining brood survival over an extended period, to determine whether there is any significant difference in survival of broods of different sizes. Walters' (1982) hypothesis that style of tending young affects clutch size also requires testing. This theory can be tested using the tritiated-water technique (Lifson & McClintock 1966) to determine the energetic costs involved in the different young-tending styles, using species that are closely related, such as the Vanellus species occupying either waterside or grassland habitats. It would also be useful to test Walters' (1982) clutch-size hypothesis with a species such as Kittlitz's Plover Charadrius pecuarius which breeds in both waterside and grassland habitats.

The tritiated-water technique can also be used to determine the energy expenditure involved in incubating eggs, which will improve the sphere of knowledge regarding both the behavioural and physiological aspects of incubation. Questions which can then be answered include why Lesser Blackwinged Plovers do not regulate their brood-patch temperatures much, yet have short incubation periods while Blackwinged Plovers control incubation periods very strongly ? Is there any energetic advantage in either strategy ? Are Lesser Blackwinged Plovers just not capable of controlling their incubation temperatures ? The use of the tritiated-water technique, however, necessitates the use of more sophisticated and dependable capture techniques than were available in this study (one of the most useful is probably a hand-held net-propelling gun) because birds were caught and injected with tritiated water (five Crowned and Blackwinged Plovers each and three Lesser Blackwinged Plovers) but could not be recaptured for analysis of water turnover.

The life-history patterns of Crowned, Blackwinged and Lesser Blackwinged Plovers, although similar in that they all have the small clutches typical of the Charadriiformes, differ in their variability in response to different environmental conditions. Lesser Blackwinged Plovers decrease their clutch size in years of poor food supply while Crowned Plovers do not alter the size of their clutches but increase their degree of iteroparity in cases of emergence of their arthropod food-supply. Blackwinged Plovers did not alter either clutch size or degree of iteroparity during the study period and there is no record of them doing so. In order adequately to study the life history of these birds a long-term study needs to be done, as Newton (1985) has done in determining the lifetime reproductive output of the European Sparrowhawk _Accipiter nisus_.

Similar studies need to be done on the biology of Crowned, Blackwinged and Lesser Blackwinged Plovers to determine the range of variation of life histories involved in each species and also to determine whether life histories change over the lifetime of a bird. In this regard the three species can be studied in different ways. Crowned Plovers are widespread in sub-Saharan Africa and should be approached in terms of whether different life-history patterns are adopted in hot arid and moist cool habitats and whether their life histories change in their exploitation of man-made habitats. Blackwinged Plovers, because there are two separate populations (one in South Africa and another in eastern Africa), could be studied from the aspect that the disjunct populations may be evolving in different directions because of different selection pressures on them. As a consequence, the life-histories of birds of the two populations may be evolving in different directions. Lesser Blackwinged Plovers, on the other hand, have a continuous distribution that is restricted to tropical and sub-tropical areas and studies should attempt to determine the stresses that act on a small bird (with a consequently large surface-area-to-volume ratio) in hot environments and how these affect their life histories, e.g. is chick survival rate lower in Lesser Blackwinged Plovers than in other, larger, grassland/woodland plovers because high temperatures causes higher casualties in Lesser Blackwinged Plovers ? If so, do they lay larger clutches in areas where environmentally-induced chick mortality is high ? In all three species a study can also be made of whether those members of the species nesting near the equator have smaller clutches than those nesting away from the equator, as has been found in many other bird species (Cody 1966). If this is so, why ?

The phylogenetic relationships of vanelline plovers are far from certain. Plumage characters have been found to contradict the relationships suggested by behavioural and morphological characters, as was found in the case of Blackwinged and Lesser Blackwinged Plovers, which were thought to constitute a superspecies on account of plumage similarities, but are behaviourally and morphologically quite different. The results of this study indicate that Crowned and Blackwinged Plovers may constitute a superspecies on account of their behavioural and morphological similarities. Further work needs to be done on the behaviour of the other species of *Vanellus* to determine the validity of the relationships found in this study. An important means of doing so might be the use of mitochondrial DNA techniques because mitochondrial DNA has been shown to evolve at a constant rate in a number of taxa (Mack *et al.* 1986) and may provide a more accurate means of determining the relationships between the species of *Vanellus*.

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APPENDIX

Mensural data: Crowned, Blackwinged and Lesser Blackwinged Plovers

Sex was determined by laparotomy, copulation position and egg-laying

	x ±S.E.	range	x ±S.E.	range	
Crowned Plover					
	Male (n=23)		**Female** (n=24)		
Weight (g)	184,40 ±2,80	155-204	178,30 ±3,80	156-204	n.s.
Wing (mm)	204,21 ±0,71	195-210	196,36 ±0,60	193-204	**
Tail (mm)	94,35 ±0,81	88-101	89,91 ±0,85	84-99	**
Tarsus (mm)	69,58 ±0,75	62-77	68,22 ±0,56	63-73	n.s.
Culmen (mm)	28,70 ±0,33	26-33	27,96 ±0,27	26-31	n.s.
Blackwinged Plover					
	Male (n=12)		**Female** (n=14)		
Weight (g)	182,80 ±4,10	167-193	173,80 ±4,12	159-182	n.s.
Wing (mm)	209,17 ±1,99	203-216	200,88 ±0,93	196-204	**
Tail (mm)	76,17 ±1,38	73-82	72,00 ±1,22	67-77	**
Tarsus (mm)	60,67 ±0,76	58-63	58,63 ±1,02	55-64	n.s.
Culmen (mm)	25,67 ±0,56	24-27	26,56 ±0,44	24-28	n.s.
Lesser Blackwinged Plover					
	Male (n=13)		**Female** (n=18)		
Weight (g)	125,75 ±2,33	118-140	116,17 ±1,72	109-126	**
Wing (mm)	181,91 ±0,80	177-186	179,93 ±1,15	172-188	n.s.
Tail (mm)	67,82 ±0,80	64-74	66,73 ±0,75	62-72	n.s.
Tarsus (mm)	61,18 ±1,09	55-67	59,73 ±0,86	56-68	n.s.
Culmen (mm)	20,45 ±0,37	19-22	20,80 ±0,42	19-23	n.s.

n.s. = no significant difference between sexes
* = difference between sexes significant at 95% level
** = difference between sexes significant at 99% level