SEXUAL DIMORPHISM AND NATAL SITE FIDELITY IN CORY'S SHEARWATER *Calonectris diomedea borialis*

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INTRODUCTION

Calonectris diomedea borealis is the North East Atlantic subspecies of the Cory's Shearwater. It is also the largest breeding Procellarid in the Northern hemisphere. It is strongly migratory, congregating to breed at specific breeding sites. Outside the breeding season, it is entirely pelagic and disperses over a vast range from subtropical waters to the temperate waters off South West Ireland and Brittany (Yesou, 1982).

Cory's Shearwater (*C.d.borealis)* possesses an impressive wingspan (male = 361 cm) and a distinctive downward-hooked bill. The overall colouring is mottled grey, the upper wing and tail being a darker brown and the underside a lighter flecked off-white (Bannerman & Bannerman, 1965).

The main NE Atlantic breeding sites are illustrated in figure 1. These islands all share a similar ecology. Their locations and climates are subtropical and they are all volcanically derived. The largest colony is that of the Salvage Islands, now a Portuguese Nature Reserve, with an estimated breeding population of 25,000 birds. Pockets of upwelling around these islands, boosting productivity, provide excellent breeding conditions for Cory's Shearwaters with their staple diet of cephalopods (Cramp & Simmons, 1977).

C.d.borealis arrives on the breeding sites from February, with numbers peaking in April-May. The breeding cycle within the colonies, from investigations

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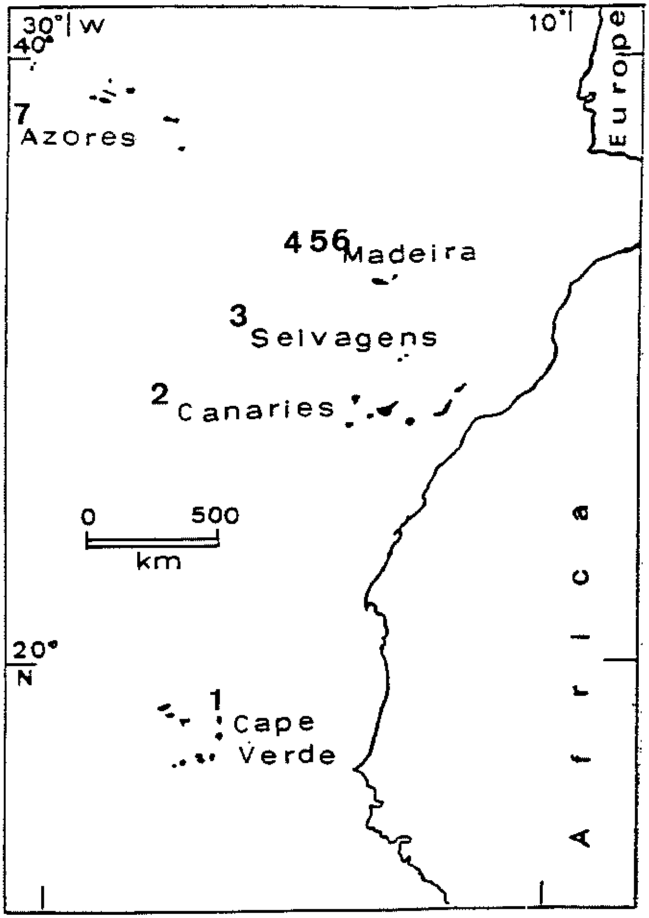

Figure 1. Breeding sites of Cory's Shearwater (*C.d.borealis*). 1) Cape Verde Archipelago; 2) Canary Islands; 3) Salvages; 4) Desertas; 5) Madeira; 6) Porto Santo and satellite islands; 7) Azores.

on the Salvages has been shown to be highly synchronous. Egg-laying and subsequent hatching throughout the colony takes place within a matter of days (Zino, 1971). Hatching occurs after a 54 day incubation period. Chicks examined within close proximity showed remarkable synchrony in their stages of development. The young Cory's fledge between October and November.

Ringing studies show that Cory's Shearwater first breed at an average age of nine years. Permanent pairs form, breeding annually and producing only a single egg. Nesting sites are various, from open ledges to abandoned rabbit burrows, cliff faces and artificial burrows from which the young are 'farmed'. Breeding failure is known to be detrimental to pair bonding and site tenacity. It has been estimated that less than 50% of failed breeders return to their nest site, with only 25% retaining their original partnership.

The basis of this project, carried out in 1986, was twofold. First, to assess whether *C.d.borealis* returns to its natal site to breed. Should this be the case, each colony is genetically discreet and may deserve subspecific status. Also, there have been reported difficulties in sexing specimens of *C.d.borealis*. Thus, the second aim of the project was to find a reliable method of sexing cases based upon the findings of Ristow and Wink (1980) of significant sexual dimorphism associated with skull and bill measurements taken from the Mediterranean subspecies *C.d.diomedea* in the Aegean Sea.

METHODS AND MATERIALS

Collections of skins and skulls of *C.d.borealis* were examined from each of the following North East Atlantic Islands (figure 1):

1. Cape Verde Islands
2. The Canaries
3. The Salvage Islands
4. The Desertas
5. Madeira
6. The Porto Santo islets
7. The Azores

Collections of skulls were made in August 1986 from the Porto Santo islets (Ferro, Baixo and Cima), Madeira (Ilheu do Agostinho and Sao Lourenço) and Deserta Grande. In Manchester the number of skulls was augmented by the stored collections in the Manchester Museum. These were samples collected from the Desertas (1981 and 1983) and the Salvages (1984). Samples for islands 1, 2 and 7 were taken from the skin collections at the Liverpool Museum and the Natural History Museum (Tring, UK). Sets of measurements were taken from the collected specimens according to those listed in Table 1 and illustrated in Figure 2.

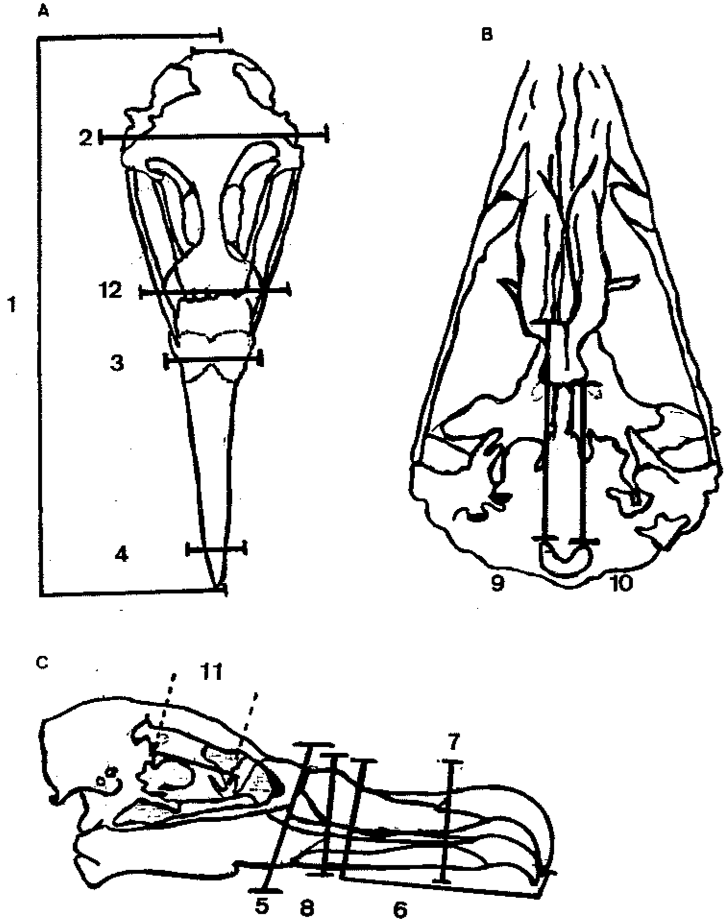

Figure 2. Measurements taken from Cory's Shearwater skulls. Variables 1-8 are the same as those taken by Ristow & Wink (1980).

The measurements from each sample were then stored on computer files according to the island from which they had been collected. The measurements of each variable and specimen were then put through Discriminant Function Analysis (using the SPSS package) to distinguish firstly the sexes on each island and secondly to distinguish between the islands. Inter-island analysis was carried out both with the sexes amalgamated and with the sexes separated. This method uses a number of measurable discriminating variables and employs them to distinguish as far as possible the groups under investigation.

PARAMETER	VAR. Nº	SAMPLE
Head Length	01	ALL SAMPLES
Head Breadth	02	
Bill Width A	03	
Bill Width B	04	
Bill Length A	05	
Bill Length B	06	
Bill Height A	07	
Bill Height B	08	
Tail Length	09	SKINS
Tarsal Length	10	
Wing Length	11	
Palate Length A	09	SKULLS
Palate Length B	10	
Eye Width	11	
Nasal Hinge	12	

Table 1. Summary of the variables used in the discriminant analysis. Variables 1 to 8 are identical to those used by Ristow & Wink (1980).

RESULTS

Fifteen characters were measured (table 1), but only those numbered 01-08 were consistently selected by the program as discriminating variables. These measurements were based upon those taken by Ristow and Wink (1980) from specimens of *C.d.diomedea* from the mediterranean. The results of the analyses are shown in figures 3-6 and tables 2-4.

Discriminant Function Analysis (SPSS) is a statistical procedure employed in phenetic analysis to separate hypothetical taxa by selecting optimally discriminating variables. Measurements taken from the selected variables are used to statistically separate each 'population' as far as possible. There was no one strongly discriminating variable but a collective combination of certain variables proved most effective in separating the various groups.

Actual Group		Predicted Group				Nº of Cases
Islands	Nº	Nº 2	Nº 3	Nº 4	Nº 7	
Canaries	Nº 2	10 83.3%	1 8.3%	0 0.0%	1 8.3%	12
Salvages	Nº 3	0 0.0%	16 94.4%	1 5.9%	0 0.0%	17
Desertas	Nº 4	1 14.3%	0 0.0%	5 71.4%	1 14.3%	7
Azores	Nº 7	0 0.0%	0 0.0%	1 25.0%	3 75.0%	4
correctly classified			85%	Nº of variables		3

Table 2. Discriminant analysis carried out on male cases from islands 2-7. Three variables were selected in order to classify 85% of the cases correctly. This illustrates the more tenacious nature of male shearwaters in terms of nesting site.

Actual Group		Predicted Group				Nº of Cases
Islands	Nº	Nº 2	Nº 3	Nº 4	Nº 7	
Canaries	Nº 2	10 66.7%	1 6.7%	2 13.3%	2 13.3%	15
Salvages	Nº 3	0 0.0%	7 70.0%	3 30.0%	0 0.0%	10
Desertas	Nº 4	1 16.7%	2 33.3%	3 50.0%	0 0.0%	6
Azores	Nº 7	0 0.0%	0 0.0%	0 0.0%	4 100.0%	4
correctly classified			68.6%	Nº of variables		4

Table 3. Discriminant analysis carried out on female cases from islands 2-7. Four variables were selected in order to classify 68% of the cases correctly. This illustrates the less tenacious nature of female shearwaters in terms of nesting site.

Actual Group		Predicted Group				Nº of Cases
Islands	Nº	Nº 2	Nº 3	Nº 4	Nº 7	
Canaries	Nº 2	21 77.8%	2 7.4%	1 3.7%	3 11.1%	27
Salvages	Nº 3	0 0.0%	18 66.7%	5 18.5%	4 14.8%	27
Desertas	Nº 4	2 11.8%	3 17.6%	11 64.7%	1 5.9%	17
Azores	Nº 7	0 0.0%	1 12.5%	0 0.0%	7 88.0%	8
correctly classified			72.15%	Nº of variables		6

Table 4. Discriminant analysis carried out on male and female cases from islands 2-7. Six variables were selected in order to classify 79 cases. The Canaries and the Azores show a higher percentage of "correct" classifications.

Sex Determination

The samples of *C.d.borealis* from the Canaries were 100% successfully grouped into male or female categories (assuming that large specimens are male, and small ones female). Discrimination was carried out upon 5 selected variables. The two most strongly discriminating variables were variable 02 (head breadth) and 01 (head length). The measurements of the Canaries specimens were taken from Museum collections of skins. Specimens from the Madeira archipelago were correctly sexed in 92% of cases, based upon 4 selected variables 06 (bill length), 04 (bill width), 01 (head length), 02 head (width). As in the cases for the Salvages the discriminant values were small and similar.

The Salvages colony is the largest undisturbed breeding colony of the NE Atlantic. Again, the variables based upon those of Ristow and Wink (1980) showed strong discriminatory values. 100% discrimination was obtained based upon 5 variables, though not the same combination as those selected for the Canaries. The highest discriminatory values were for variable 03 (bill width), 08 (bill height) and 02 (head breadth). The discriminant value of each variable is small and similar, emphasising the shared discrimination between values.

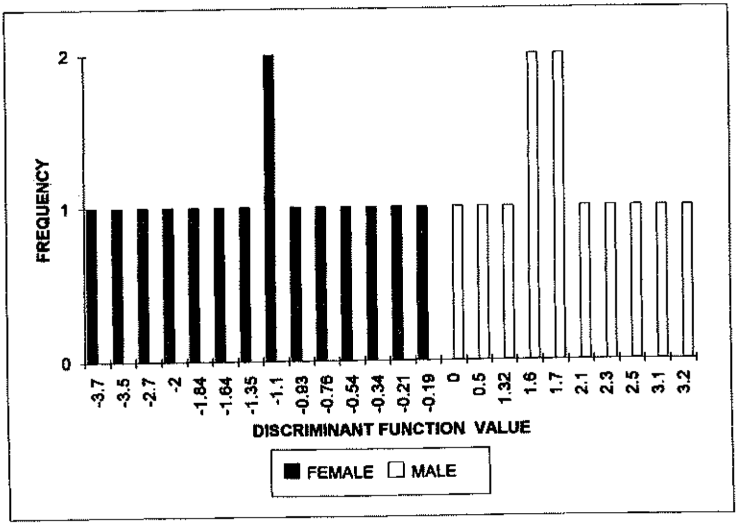

Figure 3. Cases from the Canaries. 100% discrimination between the sexes was achieved using 5 selected variables.

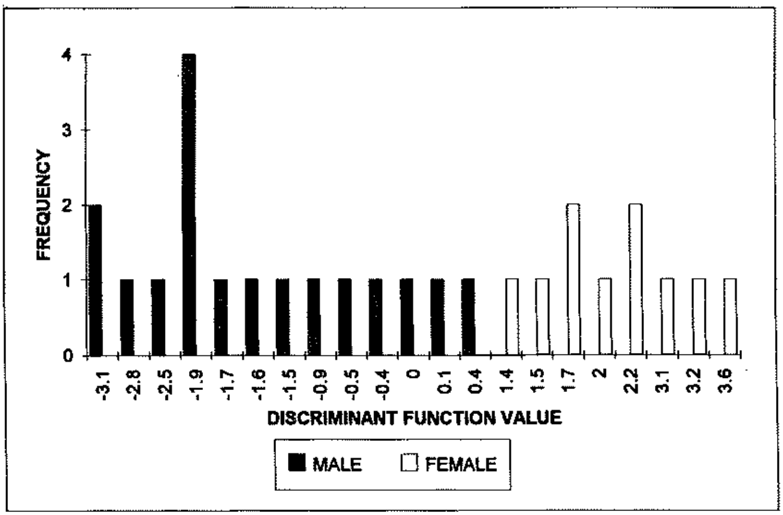

Figure 4. Cases from the Salvages. 100% discrimination between the sexes was achieved using 5 selected variables.

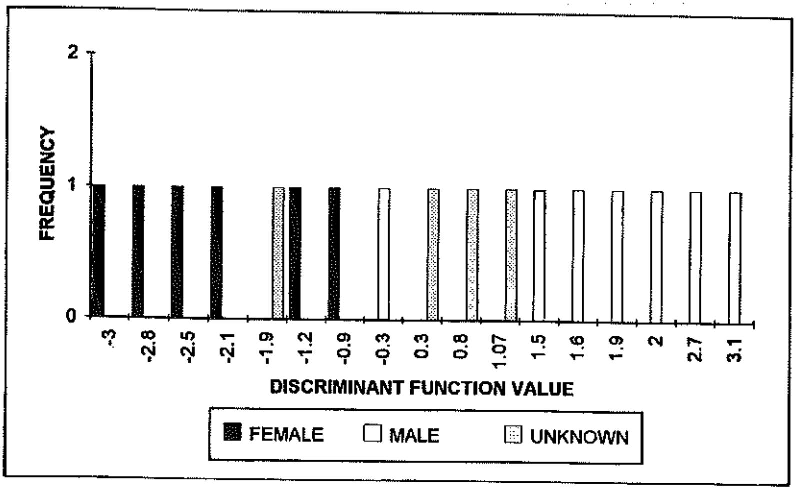

Figure 5. Islands 4,5 & 6. 92.3% Discrimination between the sexes was achieved using 4 selected variables.

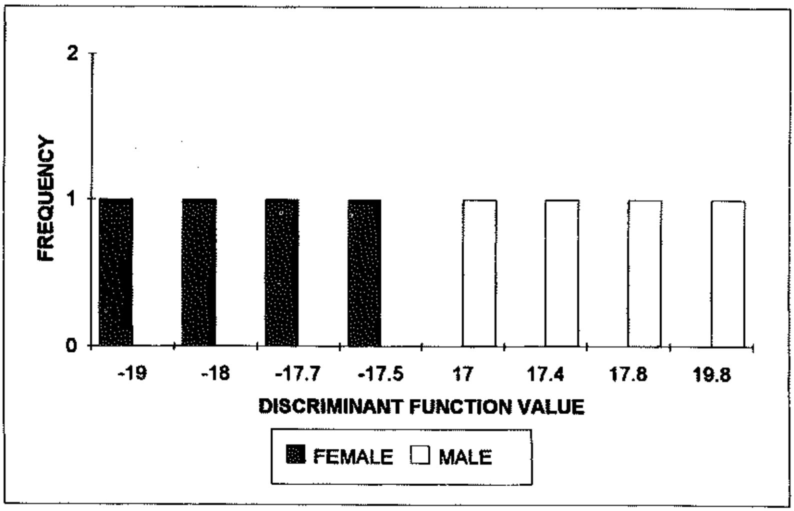

Figure 6. The Azores. 100% discrimination between the sexes was achieved using 5 selected variables. The small sample size (8) must be taken into account.

The Azores sample consisted of only 8 skins, statistically insufficient for comprehensive results. However, 100% classification was obtained based upon three selected variables 08 (bill height), 06 (bill length) and 07 (bill height).

The cases from the Cape Verde Archipelago were excluded from the study mainly because they were so distinct that they absorbed most of the discriminatory power of the SPSS programme distorting the results for the other analyses.

From the graphs of the results, it can be seen that skull and bill measurements show good discriminant value between the sexes and therefore may be seen as a sexually dimorphic feature. Table 5 illustrates the number of times each variable was selected for Discriminant Analysis.

Together, the length and width of the head and bill indicate strong sexual dimorphism. Scatterplots (figures 7 & 8) illustrate the degree of dimorphism exhibited by certain skull features. The results show that the dimorphic features are complex and that effective sexing of specimens can best be achieved by measuring several head and bill dimensions. The males exhibit greater head and bill dimensions compared to the females.

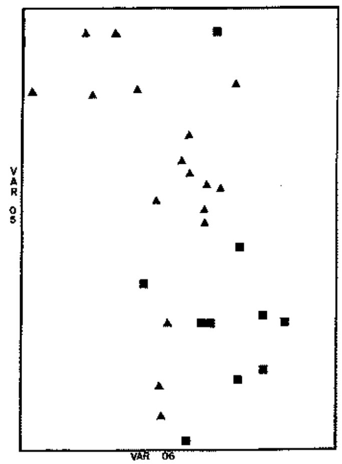

Figure 7. Two measurements of bill length (vars 05 and 06) of males and females from the Salvages. (▲=males; ■=females).

In the field, such variables can be taken from captured or collected specimens (ie live specimens or collected skeletal material) to reliably sex the individual. Perhaps with practice a trained eye could separate the sexes in the field, particulary if faced with specimens of each sex. If not, the cases can be grouped later through Discriminant Analysis.

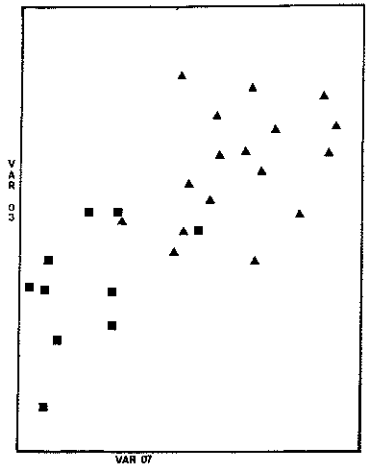

Figure 8. Bill width (var 03) and bill height (var 07) of males and females from the Salvages. (▲=males; ■=females).

Inter-Island discrimination

Discrimination Analyses were made with the sexes combined and separated. The results of inter-island discrimination with the sexes combined were not particularly conclusive for a number of reasons. Firstly, the fact that the variables were taken from a range of skins and skulls must have resulted in some scatter of the results. Secondly, the combined variables of the sexes probably muddled clear inter-island analysis.

Separation of the sexes for inter-island analysis resulted in far more definitive inter-island analysis, but especially so in the cases of the male *C.d.borealis*. This could be indicative of greater site tenacity in the case of the males compared to the females, resulting in a closer degree of relatedness among males. This phenomenon is in accordance with data and observations on avian breeding and dispersal activity.

PARAMETER	VAR. Nº	Nº of SELECTIONS
Head Length	1	6
Head Width	2	6
Bill Width A	3	6
Bill Width B	4	6
Bill Length A	5	3
Bill Length B	6	5
Bill Height A	7	5
Bill Height B	8	4
Tail Length	9	2
Tarsal Length	10	2
Wing Length	11	3
Palate Length A	9	2
Palate Length B	10	1
Eye Socket Width	11	1
Nasal Hinge Width	12	1

Table 5. The number of times each variable was selected as a discriminating variable

Using four selected variables, 68.57% of the female cases were assigned to a particular breeding colony. The discrimination was made upon 4 selected variables, 01 (head length), 02 (head breadth), 04 (bill width) and 05 (bill length).

The male cases however, showed far stronger inter-island discrimination. The selected variables O2 (head length), 03 (bill width) and 06 (bill length) indicate that good island separation can be obtained with a low number of variables.

With these selected variables 85% of the male cases were strongly linked with particular breeding sites. A comparison between the male cases of the

Salvages and the Madeira Archipelago showed very strong discrimination with 90.63% of the cases being correctly assigned to the islands under study based upon the discriminant power of only two variables 04 (bill width) and 09 (palate length). From the scatterplots (figure 9) it seems that the males from the Salvages have longer narrower bills than those from Madeira.

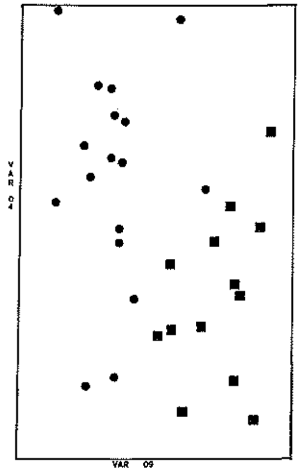

Figure 9. Bill width (var 04) and palate length (var 09) of males from the Madeira Archipelago (●) and the Salvages (■).

Thus from the inter-island analysis female *C.d.borealis* display a greater tendency to disperse compared to male *C.d.borealis*. The male of the species shows greater natal site fidelity and therefore has greater discriminant value in separating the NE Atlantic breeding sites.

DISCUSSION

Avian male philopatry and female dispersal is a well known and documented phenomenon. There are two main schools of thought upon this effect. Firstly, Greenwood's (1978) theory of group selection and secondly Baker's (1980) theory of dispersal through ontogenetic learning through familiarisation and migration. As well as these two hypotheses concerning dispersal and site fidelity, the effect of breeding failure upon dispersal must also be considered.

Greenwood considers two factors contribute to female dispersal:

1. Natal Dispersal - the movement of female juveniles from their natal site to a breeding site.

2. Breeding Dispersal - the movement of females having already bred to another breeding site.

According to Greenwood, natal dispersal is an attempt by females to reduce inbreeding at natal sites. Subsequent breeding dispersal is regarded as a population density regulator in that at maximum population densities inferior breeders such as younger inexperienced or subordinate birds are forced from the breeding colony. This argument contains two main weaknesses. Even if inferior breeders were forced to disperse there is no certainty that they will breed successfully elsewhere. Young Procellariiformes are generally bad breeders with a high failure and subsequent divorce rate (Mougin et al, 1984). However, with age and practice they increase their rate of breeding success and form permanent pairs. Also, this theory assumes that dispersal only takes place at times of increased population capacity.

Greenwood regards male philopatry as a balance to female dispersal to counteract inbreeding. When males return to their natal site, they are 'assisted' in acquiring a nest site by the fact that closely related males occupy the surrounding sites. There is no evidence of territoriality or kin selection in *C.d.borealis* although individual birds have been seen to drive away unfamiliar birds.

Baker (1980) states that avian dispersal and philopatry are based upon age, experience, and facets of migration and navigation. Immature breeders are subject to a number of dispersive factors effective over a long pre-breeding period of at least six years. During this time, Cory's Shearwaters experience exploratory migration beyond their familiar range to wintering areas etc.; this is when their navigational skills are developed.

Removal migration defines the movement of individuals from their natal site to similar sites that have been discovered through exploration and migration as navigational, feeding and breeding skills have been developed. Such migration would present no problem to a truly pelagic bird such as *C.d.borealis*. Also, accidental migration will have a dispersive effect.

The greater dispersive tendency of female *C.d.borealis* is possibly due to their greater parental investment, ie the energy invested in the production of a single egg. Since *C.d.borealis* only breeds annually, producing a single egg, the females investment is great and must pay off. With their acquired knowledge of breeding sites and their resources females can make an assessment of the different sites. The philopatric males with a sound knowledge of their natal site are a good indicator to the more dispersive female of a site's potential for successful breeding. Successful breeding would lead to strong bonding between partners and greater site fidelity. "Territoriality" is explained as defence by philopatric males against males that, due to breeding failure, have left their natal sites to stake their claim elsewhere.

Breeding failure usually leads to divorce in breeding pairs and is a major dispersive agent. Mougin et.al. (1984) claim that within the Selvagem Grande colony, non-breeding occurs in up to 4% of *C.d.borealis* reproductive lifecycle. Breeding failure results in a significant decrease in site tenacity and bonding. Only 43% of failed breeders returned to their nest site and only 25% of original pairs reformed.

CONCLUSIONS

Discriminant Analysis carried out on sexual dimorphism in *C.d.borealis* show that head and bill measurements can be reliably applied to separate the sexes. Results show that the male of the species has overall greater head and bill dimensions. Measurements taken in the field can now be used to sex specimens of *C.d.borealis*.

Inter-island analyses revealed that females have a far greater tendency to disperse compared to the philopatric males. Pair bonding and breeding success are vital in site fidelity. Inter-island separation can be carried out far more reliably when Discriminant Analysis is applied to male cases because of their tendency to breed at their natal site. Sub-speciation may occur where generations of successful breeding pairs have remained at specific breeding sites forming discreet genetic pools. The strong discrimination between specimens from the Salvages and the Madeira Archipelago may be evidence of incipient sub-speciation. The suitability of the Salvages is reflected in the large number of breeding pairs. If breeding success is high there, the breeding population is stable and consists of established pairs that return year after year to the same breeding site.

Whether sub-specific status can be assigned to any of the North-Eastern Atlantic colonies requires more detailed studies. Gel electrophoresis studies of blood or feather proteins for example may reveal more detailed genetic distinctions that are not uncovered by gross phenotypic investigations.

REFERENCES

Baker, R.R.:
1978. *The evolutionary Ecology of Animal Migration.* Hodder and Stoughton, 500 pages.

Bannerman, D.A. & Bannerman, W.M.:
1965. *The Birds of the Atlantic Islands.* Volume 2, A History of the Birds of Madeira, the Desertas, and the Porto Santo Islands. Oliver & Boyd, Edinburgh and London. 207pp.

Cramp, S. & Simmons, K.E.L.:
1977. *The Birds of the Western Palearctic,* Vol.1. Oxford University Press. pp.137-140.

Greenwood, P.L.:
1980. Mating Systems, Philopatry and Dispersal in Birds and Mammals. *Animal Behaviour* 28, 1140-1162.

Mougin, J., Roux, F., Stahl, J.C. & Jouanin, C.:
1984. Les années sabbatiques des puffins cendres reproducteures de l'ile Selvagem Grande. *C.R. Acad. Sci Paris* 299 serie III (0):147-150.

Ristow,D. & Wink, M.:
1980. Sexual Dimorphism of Cory's Shearwater. *Ill-Merrill* 21:9-12.

Yesou, P.:
1982. A propos de la Presence remarquable du Puffin Cendre C.d. prés des côtes du Golfe de Gascogne et la Mer Celtique en 1980. *L'Oiseau et la Revue Francaise d'Ornithologie,* 52, no. 3.

Zino, D.A.:
1971. The Breeding of Cory's Shearwater on the Salvage Islands. *Ibis* 113:212-217.