# Sex Determination of Great Cormorants (*Phalacrocorax carbo sinensis*) using Morphometric Measurements


VASILIOS LIORDOS[1,2] AND VASSILIS GOUTNER[1]

[1]Department of Zoology, School of Biology, Aristotelian University of Thessaloniki, GR-54124 Thessaloniki, Greece

[2]Present address: P.O. Box 80705, GR-18510 Piraeus, Greece
Internet: liordos@yahoo.com



**Abstract.**—Great Cormorant (*Phalacrocorax carbo*) is monomorphic in plumage such that sexes cannot be separated by plumage characteristics. In contrast, it displays sexual size dimorphism, with males generally being larger than females. Sexual dimorphism and variability in size of the continental Great Cormorant (*P. c. sinensis*) was studied in Greece to develop useful sexing techniques using morphometric measurements. Body mass, wing, culmen, and tarsus length of 81 birds controlled under license were measured during the wintering season in 1999-2002. The sex of each bird was determined by dissection and gonadal inspection. Forward stepwise discriminant analyses were performed to provide reliable functions that would enable the prediction of sex of a bird. Differences in size between adult and juvenile birds were not significant in both sexes, whereas males were larger than females in all measurements. Body mass (19.2%) and culmen length (11.1%) were the most dimorphic variables of those looked at followed by tarsus (6.5%) and wing (6.1%) length. Although wing length was the least dimorphic variable, it also displayed the lowest coefficient of variation (2.3%) thus being the best single measurement for separating the sexes. Three discriminant functions that correctly classified 92.6-95.1% of Great Cormorants of this sample were produced. These functions were reliable (similar accuracy for discriminant analysis and jackknife validation) and seasonally unbiased, as body mass was excluded from the analyses. The function including wing and culmen length as variables showed somewhat lower accuracy when tested with a new sample from The Netherlands suggesting that the obtained functions should be applied with caution to other populations, especially within the area of overlap between the sexes, unless inter-population sources of variation (e.g., geographic variation, hybridization, inter-observer bias) are sufficiently understood.


*Received 2 May 2007, accepted 26 November 2007.*

**Key words.**—Great Cormorant, morphometrics, sexual size dimorphism, discriminant analysis, Greece, *Phalacrocorax carbo sinensis.*

Waterbirds 31(2): 203-210, 2008


Distinguishing the sex of animals is essential for studying the structure, dynamics, habitat use, mating systems and behavior of natural populations (Hughes 1998) and sexual differences in size are widespread among animals, with males being often larger than females in vertebrates (Andersson and Norberg 1981). Many bird species, such as cormorants and shags, are sexually monomorphic in plumage, and sexes cannot be separated using plumage characteristics, but exhibit sexual size dimorphism in certain body measurements (Croxall 1995). It is possible to determine the sex of individual birds by differences in copulation and courtship behaviors (Catry *et al.* 1999) or by cloacal examination (Boersma and Davies 1987; Gray and Hamer 2001), but these methods are applicable only during the breeding season. Many researchers have used discriminant analysis to facilitate sex identification of monomorphic in plumage but dimorphic in size bird species using morphometric measurements (van Franeker and ter Braak 1993; Glahn and McCoy 1995; Weidinger and van Franeker 1998; Mallory and Forbes 2005; Svagelj and Quintana 2007). A function that includes the variables that best predict the sex from a sample of individuals of known sex is developed by this method (McGarigal *et al.* 2000). This function can subsequently be used for the identification of the sex of unknown individuals.

The Great Cormorant (*Phalacrocorax carbo*) is a large fish-eating colonial waterbird with an almost cosmopolitan distribution (Orta 1992). Two subspecies occur in Europe: *P. c. carbo* which occurs mainly along the North Atlantic coasts, and *P. c. sinensis* which is found in continental Europe and Asia with the former being larger than the latter (Newson *et al.* 2004). Besides subspecific differences in size, there are also differences between the sexes within each subspecies, with males generally being larger and heavier than females (Cramp and Simmons 1977; Johnsgard 1993). Koffijberg and van Eerden (1995) conducted the only other known study on sex identification of *P. c. sinensis*, at Lake IJsselmeer, The Netherlands.

The aim of this paper was to: 1) compare measurements of four commonly used body characters of the *P. c. sinensis* subspecies (hereafter Great Cormorant) from four major wintering areas of Greece to reveal potential significant differences in size between age (adult and juvenile) and sex (male and female) classes, 2) assess sexual size dimorphism and variability of measurements taken, 3) perform discriminant analysis to develop functions useful for discriminating sex using simple morphometric measurements, and 4) test the utility of the discriminant functions to other populations using a set of measurements of Great Cormorant external characteristics from Lake IJsselmeer, The Netherlands.

## METHODS

### Study Area

Great Cormorants controlled under license by the Ministry of Rural Development and Food were made use of during the wintering period from the Axios and Evros Deltas, the Messolonghi Lagoon, and the Amvrakikos Gulf, all sites designated as Wetlands of International Importance under the Ramsar Convention. The Axios Delta (40°27'-40°38'N, 22°33'-22°52'E) belongs to a large wetland complex covering a total of 68.7 km$^2$, situated near the city of Thessaloniki. The Evros Delta at the Greek-Turkish border (40°44'-40°51'N, 25°53'-26°8'E) is an extensive area (190 km$^2$) diverse in habitats. The Messolonghi Lagoon (37°40'-39°40'N, 20°10'-21°30'E) belongs to the largest Greek wetland complex, situated in southwest Greece, totaling 258 km$^2$. The Amvrakikos Gulf, in western Greece (38°59'-39°11'N, 20°44'-21°07'E), is the largest closed gulf in Greece, communicating with the Ionian Sea through the Aktion Strait and covers a total of 405 km$^2$.

### Sampling, Age and Sex Determination

A total of 81 birds were controlled under license during the wintering season: 13 birds from the Axios Delta (October 2001), 28 from the Evros Delta (December 1999), 16 from the Messolonghi Lagoon (February 2002), and 24 from the Amvrakikos Gulf (February 2002). Controlled birds were used for the study of several aspects of Great Cormorant ecology and biology, including diet, contaminants, body condition, and parasite census. Morphometric measurements were taken upon collection. Age was determined by examination of plumage characteristics. Juveniles (first winter) have dull buff or pale brown breast with mottles of the same color on flanks and lateral tail coverts and the rest of the underparts dull white, contrasting with the velvety black underparts of adults (Cramp and Simmons 1977). Subsequently the specimens were tagged with an identification number and then stored in a freezer at -20°C. On the day of analysis, the birds were thawed, dissected, and sexed by gonadal inspection.

### Morphometric Measurements

Four body measurements were taken. Fresh body mass was measured to the nearest 25 g with a five-kg Pesola spring balance (measurements were taken halfway to the 50-g division of the balance, when necessary, to increase accuracy). Culmen length (the upper mandible of the bill, from tip to first feathers), and tarsus length (from middle of midtarsal joint to distal end of tarsometatarsus, with foot closed towards tail) were measured with digital calipers to the nearest 0.01 mm. Wing length (from carpal joint to tip of longest primary of flattened and extended closed wing) was measured with a ruler to the nearest one mm. All measurements were taken by the same person (Vasilios Liordos) to eliminate variation among investigators.

### Data Analysis

Multivariate analyses of variance (MANOVAs), followed by one-way ANOVAs when results were significant, were performed on both age and sex to reveal differences in morphometric variables (Sokal and Rohlf 1995). Sexual size dimorphism index was calculated as: SSD = $\{(\bar{x}_m - \bar{x}_f)/\bar{x}_f\} \times 100$ (from Weidinger and van Franeker 1998), where $\bar{x}_m$ and $\bar{x}_f$ are the mean values of males and females respectively. Coefficients of variation ($CV = (SD/\bar{x}) \times 100$), where $SD$ is the standard deviation and $\bar{x}$ the mean value of either sex, were calculated for each sex and then averaged between them (Fletcher and Hamer 2003) to assess the degree of variability of each measurement (Sokal and Rohlf 1995).

Forward stepwise discriminant analysis was applied to our sample (81 individuals; 34 male and 47 female) to obtain mathematical functions that would allow one to predict the sex of a bird, in which each variable is introduced into the function, in order of maximum discriminatory power (measured by the overall Wilk's lambda), until there is no variable left with an F-value at least as significant as 0.05. Body mass is more prone to vary due to factors such as season, food availability, and time interval between last feeding and time of bird collection (Croxall 1995; Grémillet *et al.* 1996), so it was excluded from the analysis to avoid bias and obtain discriminant functions that could be used for sexing birds throughout the year. The discriminatory power of each variable (univariate discriminant analysis) was also evaluated. Discriminant analysis provides individual discriminant scores for each bird and then scores are partitioned into male and female groups based on known sexes. The cutoff point to assign individuals to male or female, for each discriminant function, was calculated as the midpoint between the mean scores for males and females, with values higher than the midpoint representing males (following van Franeker and ter Braak 1993).

The effectiveness of each discriminant function was tested with three methods. First, a 'self test' was conducted, which used all the data on which the function was performed. Second, a 'jackknife validation' was used, in which each case is classified by the functions derived from all cases other than that case. Third, an 'outgroup test' was applied, using a dataset of two morphometric variables (culmen and wing length) for 116 Great Cormorants collected throughout the year at Lake IJsselmeer, The Netherlands, during 1980-1985 (Koffijberg and van Eerden 1995). Testing discriminant functions with data that were not used to generate the functions is the best indicator of performance but it is susceptible to researcher-induced bias, because measurements were taken by different individuals.

The data satisfied all the assumptions necessary for performing discriminant analysis (McGarigal *et al.* 2000). Variables were tested for normality and tests indicated that none deviated significantly from normality (Kolmogorov-Smirnov test, $P > 0.20$ for all variables). There was also no significant difference between the covariance matrices for the sexes (Box's $M = 4.55$, $P = 0.62$), and within-sex correlation coefficients were low (maximum 0.362), showing that there was little collinearity. All statistical analyses were performed with SPSS statistical software, Version 14.0 (SPSS, Inc., Chicago).

## RESULTS

Adult and juvenile birds did not differ significantly in size in both males (MANOVA, $F_{4,29} = 0.11$, $P = 0.977$; Table 1) and females (MANOVA, $F_{4,42} = 0.91$, $P = 0.465$; Table 2). Age groups were therefore pooled together for testing differences in size between the sexes. Although some overlap in range occurred, statistical analysis showed that males were significantly larger than females (MANOVA, $F_{4,76} = 63.54$, $P < 0.001$; Table 3) in all morphometric variables (one-way ANOVAs, $F_{1,79} > 34.30$, $P < 0.001$ in all cases). Sexual size dimorphism was most pronounced in body mass, followed by culmen, tarsus and wing length in decreasing order of magnitude (Table 3). Within-sex variation was highest in body mass and lowest in wing length (Table 3).

All univariate discriminant analyses were significant ($P < 0.001$ for all analyses; Table 4). Wing length was the most powerful single discriminator, correctly classifying 91.4% of Great Cormorants (Table 4). Great Cormorants with wing length larger than 339 mm (cut-off point) were classified as males while those with smaller as females. Culmen (cut-off point = 66.90 mm) and tarsus (cut-off point = 67.31 mm) length had similar accuracy (both predicted correctly the sex of 88.9% of Great Cormorants; Table 4). Jackknife validation tests produced the same classification results as those produced by discriminant analyses for culmen and tarsus length, but not for wing length, where one more male was misclassified as female (Table 4). Outgroup cross-validation tests provided somewhat lower classification rates for wing and culmen length than the self and jackknife validation tests, with wing length being the best single discriminant for the Dutch Great Cormorants (Table 4).

Multivariate discriminant analysis applied to wing, culmen, and tarsus length provided one significant function ($P < 0.001$, Table 4) that required all the variables to separate the sexes:

$$D_1 = (\text{Wing length} \times 0.073) + (\text{Culmen length} \times 0.123) + (\text{Tarsus length} \times 0.310) - 53.693$$

This function, with a cut-off point of 0.294, correctly classified 95.1% of the 81 Great Cormorants (Table 4), misclassifying only two males and two females (Fig. 1A).

Discriminant analysis applied to culmen and tarsus length provided the following significant function ($P < 0.001$, Table 4):

$$D_2 = (\text{Culmen length} \times 0.228) + (\text{Tarsus length} \times 0.358) - 39.079$$

This function (cut-off point = 0.250), correctly classified 93.8% of the 81 birds (Table 4), misclassifying two males and three females (Fig. 1B).

**Table 1. Morphometrics of 34 male Great Cormorants collected in Greece. All measured characteristics did not differ significantly between age groups (MANOVA, P = 0.977).**

| | Adult males (N = 10) | | | Juvenile males (N = 24) | | |
|---|---|---|---|---|---|---|
| Morphometric variable | Mean | SD | Range | Mean | SD | Range |
| Body mass (g) | 2,447 | 376 | 2,000-3,000 | 2,379 | 301 | 1,900-2,900 |
| Wing length (mm) | 352 | 11 | 335-367 | 350 | 7 | 332-367 |
| Culmen length (mm) | 70.52 | 3.20 | 67.00-76.81 | 70.46 | 2.76 | 64.36-73.63 |
| Tarsus length (mm) | 69.64 | 1.48 | 66.62-71.77 | 69.27 | 2.05 | 64.45-73.40 |

**Table 2. Morphometrics of 47 female Great Cormorants collected in Greece. All measured characteristics did not differ significantly between age groups (MANOVA, P = 0.465).**

| | Adult females (N = 26) | | | Juvenile females (N = 21) | | |
|---|---|---|---|---|---|---|
| Morphometric variable | Mean | SD | Range | Mean | SD | Range |
| Body mass (g) | 2,068 | 241 | 1,600-2,500 | 1,946 | 296 | 1,500-2,500 |
| Wing length (mm) | 332 | 6 | 321-343 | 329 | 8 | 315-341 |
| Culmen length (mm) | 63.62 | 2.52 | 58.69-68.46 | 63.26 | 3.31 | 54.03-68.55 |
| Tarsus length (mm) | 65.14 | 1.41 | 61.75-67.31 | 65.12 | 1.98 | 62.00-69.23 |

Finally, a discriminant analysis using wing and culmen length was performed to obtain significant functions for comparison with the Dutch dataset. The analysis resulted in one significant function (P < 0.001, Table 4) with a cut-off point of 0.248, correctly classifying 92.6% of the 81 birds (Table 4), misclassifying four males and two females (Fig. 1C):

$$D_3 = (\text{Wing length} \times 0.085) + (\text{Culmen length} \times 0.195) - 41.816$$

Jackknife validation tests produced the same classification results as those produced by discriminant analyses for functions $D_1$ and $D_3$, whereas for $D_2$, results were slightly different (one more female was misclassified as male, Table 4). Available data allowed the application of outgroup cross-validation only to function $D_3$. Results provided lower classification rates (82.2%) than the self and jackknife validation tests (both 92.6%, Table 4). All discriminant functions obtained tended to identify females better than males, except function $D_2$ where classification rates were slightly higher for males than females (Table 4), attributed mainly to small males being classified as females.

## DISCUSSION

Body measurements of Great Cormorants taken in this study were similar to those given by Cramp and Simmons (1977), Johnsgard (1993) and Koffijberg and van Eerden (1995) for *P. c. sinensis*. *P. c. sinensis* is smaller than *P. c. carbo* in several body characters, although there is much overlap between them (Cramp and Simmons 1977; Johnsgard 1993). Newson *et al.* (2004) examined variability in biometrics in Europe and produced discriminant functions to assign known sex Great Cormorants controlled in England during the winter to *sinensis* or *carbo* subspecies.

No significant differences in morphometric measurements were found between juveniles and adults in this study. Cramp and Simmons (1977) reported that juveniles and adults are similar on average in measurements and Koffijberg and van Eerden (1995) also did not find any significant differences between age groups in their study of *P. c. sinensis* at Lake IJsselmeer, The Netherlands. In contrast, differences in all body measurements between the sexes were found significant, with males being larger and heavier than females. Sexual differences in size have also been reported previously for the Great

**Table 3. Morphometrics of 81 male and female Great Cormorants collected in Greece. Coefficients of variation (CV) and sexual size dimorphism (SSD) are also given. All measured characteristics differed significantly between the sexes (MANOVA, P < 0.001; one-way ANOVAs, $F_{1,79}$ > 34.30, P < 0.001, all tests).**

| | Males (N = 34) | | | Females (N = 47) | | | | |
|---|---|---|---|---|---|---|---|---|
| Morphometric variable | Mean | SD | Range | Mean | SD | Range | CV (%) | SSD (%) |
| Body mass (g) | 2,399 | 321 | 1,900-3,000 | 2,013 | 271 | 1,500-2,500 | 13.4 | 19.2 |
| Wing length (mm) | 351 | 8 | 332-367 | 331 | 7 | 315-343 | 2.3 | 6.1 |
| Culmen length (mm) | 70.48 | 2.85 | 64.36-76.81 | 63.46 | 2.87 | 54.03-68.55 | 4.3 | 11.1 |
| Tarsus length (mm) | 69.38 | 1.89 | 64.45-73.40 | 65.13 | 1.67 | 61.75-69.23 | 2.6 | 6.5 |

**Table 4. Classification accuracy of single measurements and discriminant functions ($D_1$, $D_2$ and $D_3$) developed for sexing Great Cormorants from Greece, according to self, jackknife and outgroup tests. Outgroup cross-validation refers to performance of single measurements and discriminant functions to a set of measurements of 116 Great Cormorants from Lake IJsselmeer, The Netherlands, taken during 1980-1985. All discriminant analyses were significant ($P < 0.001$).**

| | | | Percent correctly classified | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Self test (N = 81) | | | Jackknife validation (N = 81) | | | Outgroup cross-validation | | |
| | Wilk's Lambda | F-value | Males | Females | Total | Males | Females | Total | Males | Females | Total |
| Wing length | 0.365 | $F_{1,79} = 137.6$ | 91.2 | 91.5 | 91.4 | 88.2 | 91.5 | 90.1 | 86.4[a] | 88.9[b] | 87.6 |
| Culmen length | 0.399 | $F_{1,79} = 118.9$ | 88.2 | 89.4 | 88.9 | 88.2 | 89.4 | 88.9 | 69.0[c] | 92.3[d] | 80.0 |
| Tarsus length | 0.409 | $F_{1,79} = 114.1$ | 85.3 | 91.5 | 88.9 | 85.3 | 91.5 | 88.9 | | | |
| $D_1$ | 0.230 | $F_{3,77} = 85.8$ | 94.1 | 95.7 | 95.1 | 94.1 | 95.7 | 95.1 | | | |
| $D_2$ | 0.291 | $F_{2,78} = 94.8$ | 94.1 | 93.6 | 93.8 | 94.1 | 91.5 | 92.6 | | | |
| $D_3$ | 0.295 | $F_{2,78} = 93.15$ | 88.2 | 95.7 | 92.6 | 88.2 | 95.7 | 92.6 | 75.4[e] | 90.0[f] | 82.2 |

[a]N = 59; [b]N = 54; [c]N = 58; [d]N = 52; [e]N = 57; [f]N = 50.

Cormorant (Koffijberg and van Eerden 1995) as well as other cormorant and shag species (Potts 1969; Bernstein and Maxson 1984; Brothers 1985; Malacalza and Hall 1988; Glahn and McCoy 1995; Casaux and Baroni 2000; Quintana *et al.* 2003; Svagelj and Quintana 2007) and confirm the hypothesis of a consistent sexual size dimorphism in the Phalacrocoracidae family (Johnsgard 1993). Body mass (19.2%) and culmen length (11.1%) were the most sexually dimorphic body characters, but wing length was the most powerful parameter in separating the sexes, followed by culmen and tarsus length. This happened because although wing length showed the least sexual size dimorphism of all parameters (6.1%), it also showed the lowest coefficient of variation (2.3%). Koffijberg and van Eerden (1995) found that wing length and bill depth were the best parameters in separating the sexes for the Great Cormorant. Other studies have also identified wing, culmen and tarsus length as important morphometric parameters to discriminate between the sexes in cormorants and shags (Malacalza and Hall 1988; Glahn and McCoy 1995; Casaux and Baroni 2000; Svagelj and Quintana 2007).

Three significant discriminant functions were produced in this study, all better predictors of sex than any single measurement, correctly classifying 92.6-95.1% of Great Cormorants. A discriminant function involving three variables ($D_1$; wing, culmen, and tarsus length) was the most accurate. Koffijberg and van Eerden (1995) provided discriminant functions with classification accuracy 89.7-96.1%, also excluding body mass from analyses. However, some authors also exclude wing length from discriminant analysis because differential wingtip wear and moult schedules affect its utility as a discriminant factor (Jodice *et al.* 2000; Mallory and Forbes 2005). Function $D_2$ (with culmen and tarsus length as discriminant variables) could therefore be considered more suitable than functions $D_1$ and $D_3$ (with wing length as one of the variables) for discriminating Great Cormorants throughout the year.

Self test and jackknife validation methods used for testing the accuracy of discriminant

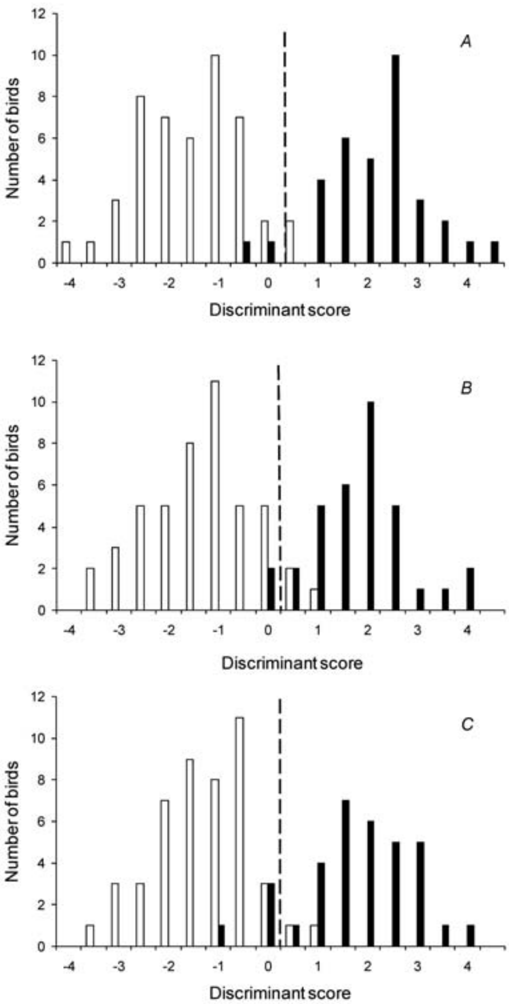


**Figure 1. Classification of male (black bars) and female (white bars) Great Cormorants collected in Greece during the wintering period, using $D_1$ (A), $D_2$ (B) and $D_3$ (C) discriminant functions.The dashed lines represent the cutt-off points, with males to the right and females to the left.**

analyses produced similar results. Gender classification accuracy suggested that a female can be identified with a slightly higher confidence than a male (correct classification rates 2.9% higher on average in females than males; see Table 4), a fact that is probably due to more size variation in the sample in males than females (see Table 3). The rates of classification accuracy are likely to be overestimated by these methods because they are applied to the sample used to generate the discriminant functions (Fox *et al.* 1981). Cross-validation with a new sample of birds measured in another place is considered as a more reliable method to test classification accuracy of discriminant functions. Using Great Cormorants measured at Lake IJsselmeer, The Netherlands, a somewhat lower correct classification rate was obtained for wing, culmen length, and function $D_3$, than those obtained by testing the functions with our own sample. Body dimensions of the birds from The Netherlands were similar to those of Greek birds, but patterns of sexual size variation were reversed, a fact probably responsible for the differences found in classification accuracy. Females had a 9% lower correct classification rate on average than males (Koffijberg and van Eerden 1995). Geographic variation in size is an important factor that may affect performance of discriminant functions (Ainley and Spear 1985; Fairbairn and Shine 1993; Leafloor and Rusch 1997). However, the geographic variation problem could be sufficiently addressed with the use of a method provided by van Franeker and ter Braak (1993) who calculated population-specific cut-off points from discriminant scores using an expectation-maximization-algorithm procedure for discriminating sexes from unknown populations without reference to sexed birds. Hybridization between the two subspecies of the Great Cormorant has been demonstrated at inland colonies in England through molecular studies (Goostrey *et al.* 1997; Winney *et al.* 2001), and may also add to variation in size where they do coexist. Discriminant functions may not be reliable if samples used contain hybrids and further research on the hybridization rate at different Great Cormorant populations and its influence on biometrics is required. Inter-observer bias is another factor that may increase misclassification of Great Cormorant sex. However, Mallory and Forbes (2005) and Donohue and Dufty (2006) found that inter-observer bias in morphometric measurements did not significantly affect gender classification rates studying Northern Fulmars (*Fulmarus glacialis glacialis*) and Red-tailed Hawks (*Buteo jamaicensis calurus*) respectively. In contrast, other studies have found measurement bias among observers (Moser and Rolley 1990; Clark *et al.* 1991).

This study described the sexual size dimorphism of Great Cormorants in Greece and provided discriminant functions that can reliably separate between the sexes, using several commonly used and easy to take in the field morphometric measurements. These functions could provide a fast, easy, non-invasive and inexpensive way to identify male and female birds in ecological studies of sex-specific differences. However, they should be used with caution to the studied as well as other *P. c. sinensis* populations, especially when the calculated discriminant scores are close to cut-off points and within the area of overlap between sexes. Ideally issues such as geographic variation, hybridization and inter-observer bias should be addressed before our functions can be reliably applied to different populations (van Franeker and ter Braak 1993; Newson *et al.* 2004).

## ACKNOWLEDGMENTS

We are very grateful to the following people for their assistance in the field and lab: S. Goutner, S. Kazantzidis, P. Menounos, D. Papandropoulos, F. Passios, F. Pergantis, P. Vafeidis and S. Zogaris. We are also indebted to M. R. van Eerden and S. van Rijn for providing us with the dataset of morphometric measurements from Lake Ijsselmeer, The Netherlands, thus allowing interpopulation comparison.

## LITERATURE CITED

Ainley, D. G. and L. B. Spear. 1985. Sexual color and size variation in the South Polar skuas. Condor 87: 427-428.

Andersson, M. and R. A. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnean Society 15: 105-130.

Bernstein, N. P. and S. J. Maxson. 1984. Sexually distinct daily patterns of Blue-eyed Shags in Antarctica. Condor 86: 151-156.

Boersma, P. D. and E. M. Davies. 1987. Sexing monomorphic birds by vent measurements. Auk 104: 779-783.

Brothers, N. P. 1985. Breeding biology, diet and morphometrics of the King Shag, *Phalacrocorax albiventer purpurascens*, at Macquarie Island. Australian Wildlife Research 12: 81-94.

Casaux, R. and A. Baroni. 2000. Sexual size dimorphism in the Antarctic Shag. Waterbirds 23: 489-493.

Catry, P., G. D. Ruxton, N. Ratcliffe, K. C. Hamer and R. W. Furness. 1999. Short-lived repeatabilities on long-lived Great Skuas: implications for the study of individual quality. Oikos 84: 473-479.

Clark, R. G., P. C. James and J. B. Morari. 1991. Sexing adult and yearling American Crows by external measurements and discriminant analysis. Journal of Field Ornithology 62: 132-138.

Cramp, S. and K. E. L. Simmons (Eds.). 1977. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Volume 1. Oxford University Press, Oxford.

Croxall, J. P. 1995. Sexual size dimorphism in seabirds. Oikos 73: 399-403.

Donohue, K. C. and A. M. Dufty Jr. 2006. Sex determination of Red-tailed Hawks (*Buteo jamaicensis calurus*) using DNA analysis and morphometrics. Journal of Field Ornithology 77: 74-79.

Fairbairn, J. and R. Shine. 1993. Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. Oikos 68: 139-145.

Fletcher, K. L. and K. C. Hamer. 2003. Sexing terns using biometrics: the advantage of within-pair comparisons. Bird Study 50: 78-83.

Fox, G. A., C. R. Cooper and J. P. Ryder. 1981. Predicting the sex of Herring Gulls by using external measurements. Journal of Field Ornithology 52: 1-9.

Glahn, J. F. and R. B. McCoy. 1995. Measurements of wintering Double-crested Cormorants and discriminant models of sex. Journal of Field Ornithology 66: 299-304.

Goostrey, A., D. N. Carss, L. R. Noble and S. B. Piertney. 1997. Population introgression and differentiation in the Great Cormorant *Phalacrocorax carbo* in Europe. Molecular Ecology 7: 329-338.

Gray, C. M. and K. C. Hamer. 2001. Food provisioning behaviour of male and female Manx Shearwaters *Puffinus puffinus*. Animal Behaviour 62: 117-121.

Grémillet, D., R. Dey, S. Wanless, M. P. Harris and J. Regel. 1996. Determining food intake by Great Cormorants and European Shags with electronic balances. Journal of Field Ornithology 67: 637-648.

Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. Ecology 79: 383-399.

Jodice, P. G. R., R. B. Lanctot, V. A. Gill, D. D. Roby and S. A. Hatch. 2000. Sexing adult Black-legged Kittiwakes by DNA, behavior, and morphology. Waterbirds 23: 405-415.

Johnsgard, P. A. 1993. Cormorants, Darters, and Pelicans of the World. Smithsonian Institution Press, Washington.

Koffijberg, K. and M. R. van Eerden. 1995. Sexual dimorphism in the Cormorant *Phalacrocorax carbo sinensis*: possible implications for differences in structural size. Ardea 83: 37-46.

Leafloor, J. O. and D. H. Rusch. 1997. Clinal variation in Canada Geese affects morphometric discrimination techniques. Journal of Wildlife Management 61: 183-190.

Malacalza, V. E. and M. A. Hall. 1988. Sexing adult King Cormorants (*Phalacrocorax albiventer*) by discriminant analysis. Colonial Waterbirds 11: 32-37.

Mallory, M. L. and M. R. Forbes. 2005. Sex discrimination and measurement bias in Northern Fulmars *Fulmarus glacialis* from the Canadian Arctic. Ardea 93: 25-36.

McGarigal, K., S. Cushman and S. Stafford. 2000. Multivariate Statistics for Wildlife and Ecology Research. Springer-Verlag, Inc., New York.

Moser, T. J. and R. E. Rolley. 1990. Discrimination of Giant and Interior Canada Geese of the Mississippi flyway. Wildlife Society Bulletin 18: 381-388.

Newson, S. E., B. Hughes, I. C. Russell, G. R. Ekins and R. M. Sellers. 2004. Sub-specific differentiation and distribution of Great Cormorants *Phalacrocorax carbo* in Europe. Ardea 92: 3-10.

Orta, J. 1992. Family Phalacrocoracidae (Cormorants). Pages 326-353 *in* Handbook of the Birds of the World, Volume 1 (J. del Hoyo, A. Elliot and J. Sargatal, Eds.). Lynx Editions, Barcelona.

Potts, G. R. 1969. The influence of eruptive movements, age, population size and other factors on the survival of the shag (*Phalacrocorax aristotelis* L.). Journal of Animal Ecology 38: 53-102.

Quintana, F., G. Somoza, M. Uhart, C. Cassará, P. Gandini and E. Frere. 2003. Sex determination of adult Rock Shags by molecular sexing and morphometric parameters. Journal of Field Ornithology 74: 370-375.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. 3rd ed. W. H. Freeman and Company, New York.

Svagelj, W. S. and F. Quintana. 2007. Sexual size dimorphism and sex determination by morphometric measurements in breeding Imperial Shags (*Phalacrocorax atriceps*). Waterbirds 30: 97-102.

van Franeker, J. A. and C. J. F. ter Braak. 1993. A generalized discriminant for sexing fulmarine petrels from external measurements. Auk 110: 492-502.

Weidinger, K. and J. A. van Franeker. 1998. Applicability of external measurements to sexing of the Cape Petrel *Daption capense* at within-pair, within-population and between population scales. Journal of Zoology, London 245: 473-482.

Winney, B. J., C. D. Litton, D. T. Parkin and C. J. Feare. 2001. The subspecific origin of the inland breeding colonies of the Cormorant *Phalacrocorax carbo* in Britain. Heredity 86: 45-53.