

Pekin ducks are the birds most often used for studies of renal (Holmes et al 1968, Gerstberger and Gray 1993) and extrarenal (Peaker and Linzell 1975) salt and water excretion in birds with salt glands. Since several studies (Hughes et al. 1989, 1992, this study) suggest that sex may influence osmoregulation in Pekin ducks, especially under conditions of saline stress, it would seem necessary to include sex as a variable when evaluating osmoregulatory responses.

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## Method for Sexing Fledglings in Cory's Shearwaters and Comments on Sex-ratio Variation

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Equal parental investment in the two sexes is a necessary consequence of natural selection (Fisher 1930). Studies of sex ratios at birth (or, in birds, at fledging) have focused particularly on sexually dimorphic species to test the prediction that there should be a bias towards the smaller, "cheaper" sex (Trivers 1972; also, see reviews in Clutton-Brock and Albon 1982, Clutton-Brock 1986, Breitwisch 1989). The prediction has been upheld in mammals, but not in birds (Clutton-Brock 1986, Breitwisch 1989, Richner 1991) and not even in species that are strongly dimorphic in size, such as raptors (Newton 1979, Edwards et al.

1988, Negro and Hiraldo 1992). In bird species that are not dimorphic in size, offspring sex ratios are poorly documented, probably because chicks are difficult to sex in the field. Methods of sexing chicks at or before fledging, therefore, are of considerable interest. In this paper, we describe the calls given by chicks in Cory's Shearwater (*Calonectris diomedea*). Using sexual dimorphism in voice, we derive a discriminant function based on morphometric measurements that allows the sex of fledglings to be determined. The sex ratio at fledging departed significantly from parity (male biased).

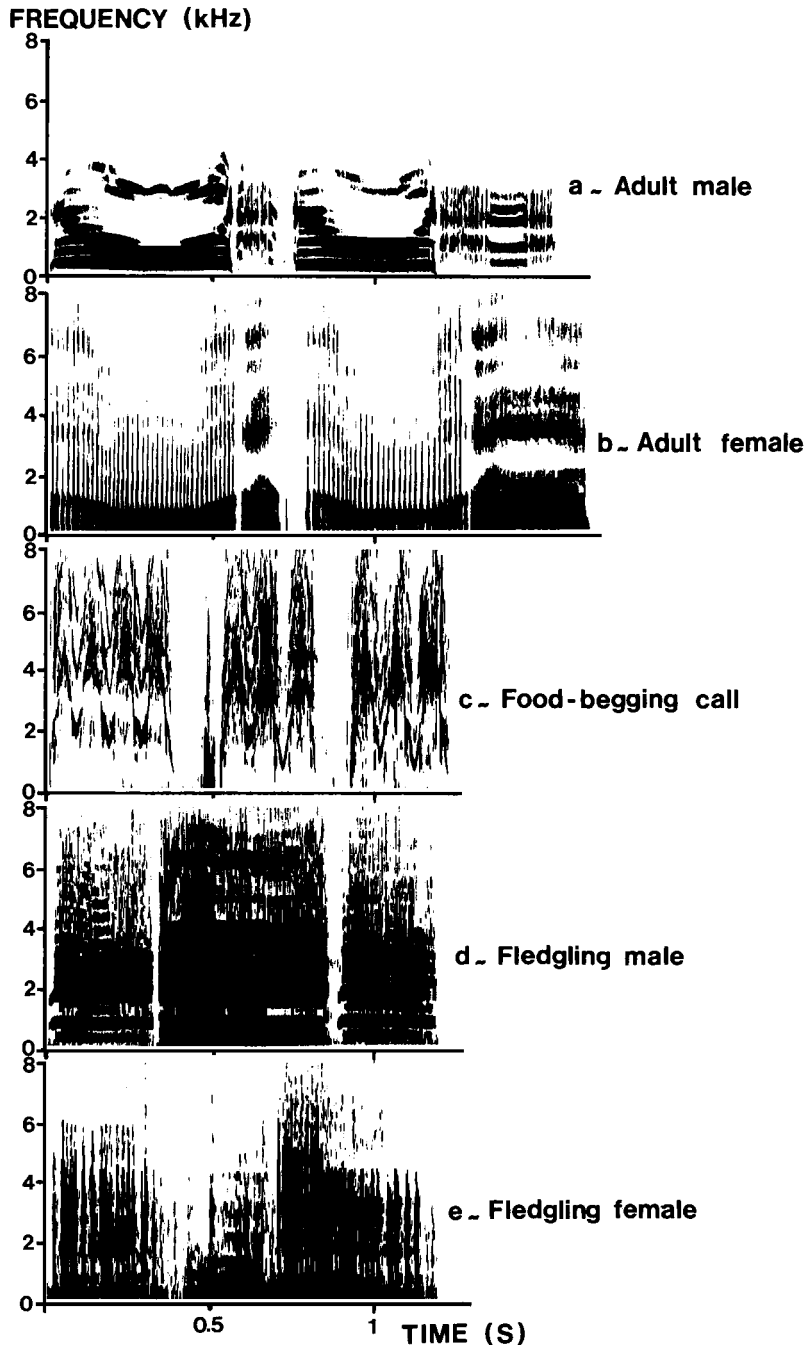


Fig. 1. Sonograms of Cory's Shearwater calls: (a) adult male; (b) adult female; (c) food begging call of the chick; (d) fledgling male; (e) fledgling female. Note similarity between adult and fledgling call for a given sex, in particular with respect to frequency spectrum. Male calls show clear spectrum with a fundamental frequency and several harmonics, while female calls show fast amplitude modulation. Time in seconds, frequency in KiloHertz.

*Methods and results.*—The study was conducted in a monospecific colony of 255 to 400 pairs of Cory's Shearwaters on Lavezzi Island (41°20'N, 09°15'S), a 66-ha natural reserve situated between Corsica and Sardinia in the western Mediterranean. The island is mainly flat, but there are several discrete blocks of granite on which are distinct subcolonies of shearwaters (for details, see Thibault 1993). Adult calls are strongly dimorphic (Ristow and Wink 1980, Bretagnolle and Lequette 1990), and significant sexual size dimorphism has been noted in adults (Massa and Lo Valvo 1986, Mougin et al. 1986, Granadeiro 1993). Chick calls, however, have not been described (except for onomatopoeic description in Cramp and Simmons 1977). We tape recorded 91 chicks with a Sony WM-D6C and a Sony ECM-929LT microphone during banding operations that were conducted from 1990 to 1994. Banding is realized during three successive days. Between 1990 and 1994, these three days ranged from 26 September to 9 October. In 1994, chicks were not tape recorded, but 29 additional chicks were heard calling. All chicks ( $n = 310$ ), whether tape recorded or not, were measured (wing length, mass, culmen and bill depth at hook).

As is the case in many petrels, Cory's Shearwater chicks use a food-begging call (Fig. 1c; Cramp and Simmons 1977) when their parents are in the burrow; this call is not sexually dimorphic. At the age of about 80 days, chicks develop another call, which eventually became similar to the adult duet call (Bretagnolle and Lequette 1990; Fig. 1a, b, d, and e). Sexual dimorphism in this call was apparent in fledglings; the same parameters (i.e. the frequency pattern; see differences in fundamental frequency in Fig. 1) are involved as in adults. Calls, therefore, appear to be reliable for sexing fledglings giving the duet call.

We then used a first set of 94 chicks that could be sexed by their voice (65 from tape recordings and 29 by ear), and submitted their measurements to a discriminant analysis. This analysis was chosen because it provided: (1) a way to check for the existence of sexual dimorphism; (2) a measure of the discriminative power of morphometric variables; and (3) a discriminant function that could be used to sex the remaining 216 chicks not heard calling. Normality of all variables was checked, permitting the use of a parametric discriminant analysis. However, within-group covariance were not homogeneous and, thus, within-group covariance matrices and quadratic discriminant function were used. The performance of the quadratic discriminant function was assessed: (1) by error-count estimates (SAS Institute 1988) calculated by applying discriminant function to same data and counting number of misclassified birds (which may result in overestimating performance of discriminant function); and (2) using crossvalidation (a technique that determines a discriminant function based on  $n-1$  birds, and then classify the remaining bird, this being done for each bird). The latter technique

TABLE 1. Results of discriminant analysis performed on morphometric variables of Cory's Shearwater fledglings ( $n = 94$ ) to separate males and females. Simple statistics and multivariate statistics given<sup>a</sup>, as well as raw canonical coefficients (axis 1 and 2) used for classification formula<sup>b</sup>.

Variable	F	Raw canonical coefficient	
		Axis 1	Axis 2
Wing (mm)	0.935 <sup>™</sup>	-0.0157	0.0412
Body mass (g)	78.43 <sup>***</sup>	0.0027	-0.0055
Culmen length (mm)	55.94 <sup>***</sup>	0.4408	-0.1538
Bill height (mm)	14.34 <sup>***</sup>	1.1532	0.7715

\*\*\*,  $P < 0.001$ ; <sup>™</sup>,  $P > 0.05$ .

<sup>a</sup> Wilk's Lambda = 0.33,  $df = 89$ ,  $P < 0.001$ .

<sup>b</sup> Obtained with a canonical discriminant analysis.

avoids overestimation of performance of the discriminant function (SAS Institute 1988). All statistical analyses were performed using SAS statistical package (SAS Institute 1988).

We found that fledglings, like adults, exhibit size dimorphism (Table 1). Only five fledglings (two females and three males) were misclassified, resulting in an error-rate estimate of 5.4% (i.e. 94.6% correctly classified). Similarly, the crossvalidation technique showed that 93.7% of the fledglings were assigned to the correct sex group. Interestingly, this is very similar to results obtained with discriminant analyses performed on the same morphometric parameters for adult birds (95.0 and 96.8%; Ristow and Wink 1980, Granadeiro 1993; Corsica unpubl. data). The discriminant function was used to sex the remaining 216 chicks, according to year and subcolony (Table 2).

The deviation of the sex ratio (expressed as percent males) from parity was tested using the binomial distribution; two-sided binomial probabilities for the given or more extreme sex ratios, the most conservative technique (Krackow 1993), were calculated. Overall (i.e. for all years and all subcolonies), there was a significantly biased sex ratio of 55.4% (Table 2). However, partitioning the data according to year and/or subcolony resulted in nonsignificant differences in all but one case, although the sex ratio was most often biased towards males (Table 2). The sample sizes for the subcolonies and years simply were too small to show significance for the relatively slight biased result.

*Discussion.*—Nearly all available evidence indicates that sex ratios at the nestling stage are unity in birds (Clutton-Brock 1986, Breitwisch 1989), the only exceptions being species that display strong sexual size dimorphism. Moreover, in birds in general, when sex ratios have been found to differ from parity at fledging, it was usually in favor of females (Clutton-Brock 1986, Breitwisch 1989, Olsen and Cockburn 1991; but

TABLE 2. Variation in percent of male Cory's Shearwater fledglings in different subcolonies and years.

	<i>n</i>	Sex ratio (%)	Breeding success
<b>Subcolony*</b>			
1	26	76.9**	0.55
2	88	52.3	0.64
3	33	57.6	0.41
4	19	52.6	0.37
5	113	56.6	0.49
6	16	43.8	0.24
<b>Year</b>			
1990	27	66.7	0.45
1991	52	63.4	0.55
1992	58	60.3	0.46
1993	87	52.8	0.57
1994	86	46.5	0.78
Total	310	55.4*	—

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; all others,  $P > 0.05$ .

\* One subcolony sampled only in 1993 and 1994 and, thus, not included in subcolony analysis.

see Zijlstra et al. 1992). The reason for such a discrepancy is thought to be that male chicks tend to be larger than female chicks and suffer a higher mortality rate during growth (Griffiths 1992). All seabirds studied so far show parity in sex ratios or, in the case of size dimorphism, a bias towards females (Ryder 1983, Hunter 1984, Griffiths 1992, Graves et al. 1993). This contrasts sharply with our results for Cory's Shearwaters, where the overall sex ratio is biased towards males (though the species is not strongly size dimorphic and males are slightly larger than females).

In general, sex ratios and sex allocation in birds are largely debated, and the possibility that these results are artifactual must be carefully examined (see Olsen and Cockburn 1991). Our first step was to sex fledglings by their calls. Calls have proven to be reliable for sexing adult Cory's Shearwaters (Ristow and Wink 1980, Bretagnolle and Lequette 1990, Granadeiro 1993) and, in fact, sexual voice dimorphism has been found in virtually all petrel species studied (for references, see James and Robertson 1985; Bretagnolle [in press] includes information on 43 species). Given the great similarity of fledgling calls to those of adults, the reliability of sexing fledglings by their calls should be as high as for adults. Furthermore, the degree of size dimorphism in fledglings is the same as in adults. Therefore, we do not think that sexing fledglings by their calls has biased our results.

The second step in our procedure was to sex fledglings that did not call using a discriminant function. We detected no significant difference in sex ratios of fledglings sexed by their calls compared to those sexed by the discriminant function ( $G$ -test,  $G = 0.538$ ,  $P > 0.5$ ). There were some errors in allocating fledglings to a given sex, but error-rate estimates were between

5.4 and 6.3%, which is approximately the deviation of sex ratio. Thus, when considering the "worst" hypothesis (i.e. the 6.3% error-rate results in all males being females, and vice versa), the overall sex ratio becomes 52.8%, which is suggestive but nonsignificant statistically ( $P = 0.18$ ). Therefore, we cannot definitely reject the possibility of the bias being caused by uncertainty of the discriminant function, though this is unlikely because the direction of the bias is almost systematically the same in different years and for different subcolonies.

Another source of potential error could be if large female fledglings were mis-sexed as males more often than small males were mis-sexed as females; this could happen if there were a different effect of age on growth according to sex (for theoretical growth curves in sexually dimorphic species, see Richner 1991). To eliminate this possible bias, we used wing length as an age indicator (see Granadeiro 1991) and controlled bill morphometrics and body mass according to wing length (following Stearns 1983). This did not change the predicted sex of any fledgling, which suggested that the bias was not an effect of age. Moreover, we failed to detect any significant effect of banding-operation dates on sex ratio, though sample size is small (Spearman's rank correlation coefficient,  $r_s = 0.1$ ,  $n = 5$ ,  $P > 0.5$ ). Thus, we conclude that the biased sex ratio is not an artifact due to the way we handled the data and/or used the discriminant function.

The ship rat (*Rattus rattus*) reached Lavezzi island at least several centuries ago (Vigne et al. 1994). Predation by rats on Cory's Shearwater chicks can be heavy, but affects breeding success differently according to year and subcolony (Thibault in press). An explanation could be that rats kill more females than males, possibly because male chicks, at least when older, are much more aggressive than female chicks (pers. obs.). Rat populations have been controlled on some of the subcolonies in recent years, allowing comparison of the sex ratio with respect to rat control. We detected no significant differences in sex ratio between the two sets (184 versus 123 fledglings,  $G$ -test,  $G = 1.59$ ,  $P = 0.21$ ). Therefore, it is unlikely that rats alone account for biased sex ratios because, although rat population density varies among subcolonies, biased sex ratios occurred at all subcolonies (Table 2).

Trivers and Willard (1973) suggested that, during periods of lower than average resource abundance, offspring sex ratio in a population should shift toward the sex with the lower reproductive variance (Howe 1977), though this has not been documented in birds (e.g. Clutton-Brock 1986, Bednarz and Hayden 1991). The sex ratio and breeding success of Cory's Shearwaters on Lavezzi Island (J.-C. T. unpubl. data) were compared over five years and between subcolonies. When we compared sex ratios and breeding success (Table 2) by year ( $r_s = -0.9$ ,  $n = 5$ ,  $P > 0.05$ ) and by subcolony ( $r_s = 0.37$ ,  $n = 6$ ,  $P > 0.05$ ), no significant correlations were found.

In conclusion, the sex ratio in Cory's Shearwater is slightly, but significantly, biased toward males at fledging. Since sex ratios may vary geographically (see Clutton-Brock et al. 1981), data from other colonies using the sexing method that we have described would be welcomed in order that firm conclusions can be drawn.

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## Responses of Snow Geese to Artificially Induced Hatching Asynchrony and Increased Clutch Size

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A common feature of precocial birds is the tendency for their clutches to hatch synchronously (Flint et al. 1994). Usually, synchronously hatching clutches have higher numbers of young leaving the nest (Clark and Wilson 1981). In clutches hatching asynchronously, late-hatched young tend to get left behind when the brood leaves the nest.

In theory, clutches can only hatch synchronously if incubation begins with the laying of the last egg, but waterfowl generally begin incubation before the laying of the last egg (Afton and Paulus 1992). In compensation, embryos in later-laid eggs exhibit accelerated hatching to some degree and hatch with the rest of the clutch (Vince 1964, Davies and Cooke 1983). Clutch size can play an important role in hatching synchrony. For example, there is more time during laying of larger clutches to initiate incubation and increase the hatching asynchrony of the clutch (Kernamer et al. 1990). Also, unequal incubation constancy of certain eggs may be more frequent in larger clutches.

Our purposes were to: (1) determine how Snow Geese (*Anser caerulescens caerulescens*) respond to experimentally induced hatching asynchrony; (2) determine if this response differed if the asynchrony was induced by extra eggs (increasing clutch size) or by swapping eggs (maintaining the same clutch size);

and (3) determine if female Snow Geese will abandon their nest if the clutch size is artificially increased.

*Methods.*—This study was performed in the summer of 1994 at La Pérouse Bay (58°43'N, 93°27'W), 30 km east of Churchill, Manitoba. A colony of Snow Geese have been studied here since 1968. A description of the study area and general field methods are included in Cooke et al. (1995).

The experimental manipulation of the Snow Goose clutches occurred on 4 June, approximately 11 days after the mean nest-initiation date of the colony. All birds in the study area had begun to incubate their clutches. We used 40 four-egg clutches in the experiment, each of which was randomly assigned to one of two manipulations: (1) additions, or (2) swaps. In the "addition nests," two eggs gathered from nearby two- and three-egg nests were added to the four-egg clutch, raising the clutch size to six. This was done to determine whether artificially enlarged clutches could be incubated successfully by Snow Geese, and what the response would be to the resulting hatching asynchrony. In "swap nests," a pair of four-egg nests were chosen, two eggs from each nest were exchanged with each other, leaving the clutch size at four eggs. An effort was made to only swap eggs of similar laying sequences; laying sequences were roughly determined by the degree of staining of the