

## Natal Philopatry and Close Inbreeding in Cory's Shearwater (*Calonectris diomedea*)

CORINNE RABOUAM,<sup>1</sup> JEAN-CLAUDE THIBAUT,<sup>2</sup> AND VINCENT BRETAGNOLLE<sup>1,3</sup>

<sup>1</sup>Centre d'Etudes Biologiques de Chizé, CNRS, F-79360 Villiers-en-Bois, France; and <sup>2</sup>Parc Naturel Régional de la Corse, BP 417, F-20184 Ajaccio, Corsica

Close inbreeding is known in several bird species, although it is seldom observed (Greenwood et al. 1978, Craig and Jamieson 1988, Gibbs and Grant 1989, Bensch et al. 1994). Inbreeding can have important evolutionary consequences because it may carry both costs and benefits to fitness (Mayr 1963, Shields 1983, Greenwood 1989). However, the seemingly low rate of inbreeding in nature may result from the fact that documenting inbreeding requires long-term monitoring of marked individuals. Colonial waterbirds are good candidates for studies of inbreeding because they often exhibit high natal philopatry (Greenwood and Harvey 1982). Moreover, long-term studies allowing individual identification and monitoring are relatively easy and widespread in this group (Wooller et al. 1992). Curiously, however, only two cases of inbreeding have been reported for colonial waterbirds: Yellow-eyed Penguin (*Megadyptes antipodes*; Richdale 1957), and Mute Swan (*Cygnus olor*; Coleman et al. 1994). Here, we report two cases of close inbreeding in Cory's Shearwater (*Calonectris diomedea*) documented during an 18-year study. We also consider philopatric behavior in this species and its possible relationships with inbreeding.

Cory's Shearwaters are highly philopatric (Ristow et al. 1990, Thibault 1993, Borg and Cachia-Zammit 1997), breeding only on islands in the Mediterranean Sea (*C. d. diomedea*), and along the west coast of Africa from the Cape Verde islands (*C. d. edwardsii*) to the Macaronesian and Berlenga islands (*C. d. borealis*). The biology of this species has been well documented, and geographic variation in biometric (Masa and Lo Valvo 1986), vocal (Bretagnolle and Lequette 1990), and genetic (Randi et al. 1989, Wink et al. 1993) traits tend to confirm this extreme philopatric behavior.

**Methods.**—Our study was conducted on the Lavezzi Islands, south Corsica (300 to 400 breeding pairs). All adults and fledglings were banded and recaptured annually between 1978 and 1996 in five subcolonies totaling 104 to 133 nests (Thibault 1993); 1,045 chicks were banded during this period. Prospecting birds also have been recaptured, albeit irregularly (but more thoroughly since 1992; see Thibault 1993). Recaptured birds were sexed using bill dimensions that have about 95% predictive power (Ristow and Wink 1980, Granadeiro 1993, Thibault 1993).

All statistics were performed using the SAS statistical package (SAS Institute 1994).

**Results.**—Males and females were caught for the first time on their natal colony at a mean of  $5.6 \pm$  SD of 1.6 years after fledging (range 3 to 12 years,  $n = 96$ ), and first breeding attempts occurred at  $7.7 \pm 2.0$  years old (range 5 to 13 years,  $n = 68$ ). No significant difference occurred between the sexes in age of first capture (males:  $5.57 \pm 1.8$  years,  $n = 68$ ; females:  $5.61 \pm 1.1$  years,  $n = 28$ ; Kolmogorov-Smirnov test,  $D = 0.187$ ,  $P = 0.49$ ) or age of first breeding (males:  $7.6 \pm 1.9$  years,  $n = 57$ ; females:  $8.0 \pm 2.4$  years,  $n = 11$ ;  $D = 0.167$ ,  $P = 0.96$ ).

We observed consistent sexual differences in natal dispersal. First, markedly fewer females returned and were recruited as breeders at their natal colony. Considering individuals banded as fledglings on Lavezzi Island, and which would have been old enough to return ( $n = 710$ ), 151 (21.3%) were recaptured at least once between 1981 and 1996, all but one on Lavezzi Island. Of these, 66.9% were males and 25.8% were females (the remaining 7.3% were of undetermined sex). Only 49.0% of these 151 fledglings subsequently were recaptured as breeders; most of them were males (82.4%). The male bias in natal philopatry was higher than that in the sex ratio of fledglings in this population (55.4% males; Bretagnolle and Thibault 1995). Second, the pattern of dispersal differed significantly according to sex in breeders ( $D = 0.550$ ,  $n = 74$ ,  $P < 0.005$ ) and nonbreeders ( $D = 0.496$ ,  $n = 96$ ,  $P < 0.001$ ; see Fig. 1). Conversely, within both sexes, we found no significant differences in the pattern of dispersal whether birds were found as nonbreeders or breeders (males:  $D = 0.147$ ,  $n = 129$ ,  $P = 0.49$ ; females:  $D = 0.111$ ,  $n = 41$ ,  $P = 0.99$ ; Fig. 1). These figures are comparable to those published by Thibault (1993) from smaller samples. Overall, both sexes exhibited very high philopatry, with more than 95% and 46% of male and female recruits, respectively, establishing within 200 m of their natal burrows. The farthest dispersal movements were limited to transfers between close subcolonies (respectively, 11.5% and 69.2% of the males and females that returned to breed), although sampling bias may have occurred (see Barrowclough 1978). However, despite extensive searches of all Corsican colonies in 1995 and 1996, only one female recruit was found in another colony, although less than 4 km from her natal site (and within the same archipelago).

Interestingly, 14.7% of the male recruits nested in their natal burrows (Fig. 1). Their age of first breed-

<sup>3</sup> Address correspondence to this author. E-mail: breta@cebc.cnrs.fr

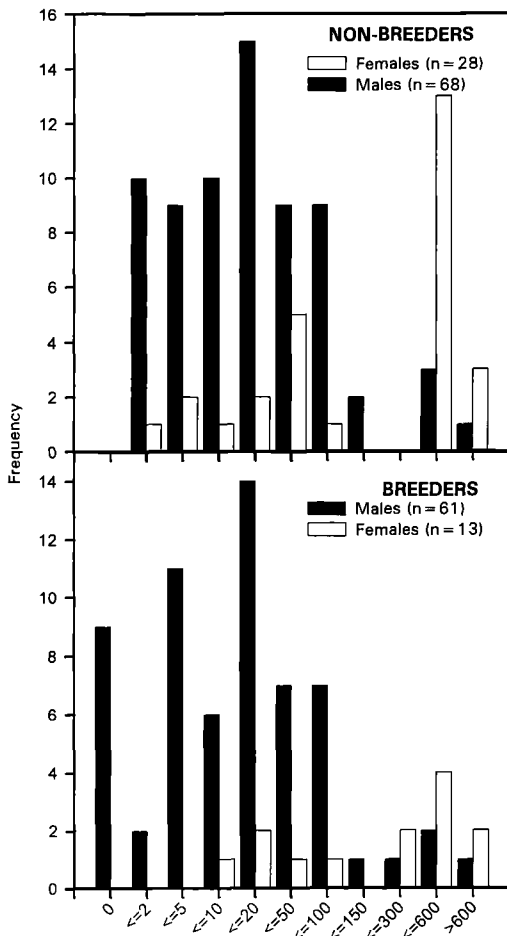


FIG. 1. Distance between natal burrow and location of recapture according to sex for nonbreeding (upper) and breeding (lower) Cory's Shearwaters.

ing ranged from 5 to 13 years. In two cases, males paired with their mothers. One was six years old, and his father had been reported dead four years before, whereas the other was 13 years old, and his father was last seen two years before in the same nest. This second male bred successfully with his mother in 1994, 1995, and 1996. Of the nine fledglings that bred in their natal nests, the fathers of six were known: five (55%) had not been seen during the last two years or more before the male recruits established, and one (11%) was breeding in an adjacent nest. Conversely, the fathers of only 23% ( $n = 52$ ) of the male recruits that bred away from their natal nests had not been seen during the last two years before establishment, whereas 33% of the fathers were still breeding in the same colony.

*Discussion.*—Our results provide the first known

cases of close inbreeding in Cory's Shearwater (another has been found in Crete; D. Ristow pers. comm.) and also are the first such cases for any species in the Procellariiformes.

A key factor promoting inbreeding is the attractiveness of the social group or the natal site, i.e. philopatry (Greenwood 1980). Sex-biased natal dispersal, as well as kin recognition, may be effective behavioral processes for avoiding close inbreeding (Ralls et al. 1986, Hoogland 1992, Bollinger et al. 1993, Wolff 1993, Lambin 1994, Pusey and Wolf 1996). Because Cory's Shearwaters settled to breed in close proximity to their natal nests, we should have expected the occurrence of inbreeding. However, the rate of inbreeding in our study was low. In colonial seabirds, competition for nesting space often is intense. Thus, the spatial pattern of recruitment to the natal colonies may be governed primarily by the availability of space. Furthermore, high levels of nest-site tenacity and mate fidelity observed in long-lived birds such as Cory's Shearwater (Mougin et al. 1987, Ristow et al. 1990, Thibault 1994) might prevent young birds from settling in or near their natal nests, thus contributing to reduced levels of inbreeding. Indeed, young male recruits were less prone to breed in their natal nests when their fathers were present in the natal colony (either in the natal nest or not). This result indicates that intrasexual competition could be an influential factor in the establishment of young males at their natal sites.

We documented only cases of sons breeding with their mothers. The lack of father/daughter pairings could have resulted from the reduced rate of recruitment of females to the natal colony and their higher level of dispersal (Ristow et al. 1990, Thibault 1993, this study). Moreover, we suggest that brother/sister pairings are not observed because each nest produces only one chick per year, and breeding is delayed until the fifth year, which reduces the chances that two siblings will meet and form a pair bond.

In conclusion, although Cory's Shearwaters show strong philopatry that results in high genetic similarity between mates (Swatschek et al. 1994), their sex-biased dispersal and mating strategies apparently ensure an optimal balance between inbreeding and outbreeding, which could serve to avoid the disruption of coadapted gene complexes and the loss of local adaptations (Bateson 1983, Shields 1983).

*Acknowledgments.*—We thank A.-M. Monnard, P. Duncan, B. Arroyo, S. J. G. Hall, and S. Waugh for improving the first draft of the manuscript. Special thanks are due to the staff of the Lavezzi Nature Reserve for accommodation and transport facilities. Fieldwork was financed by the "Comité Scientifique de l'Association de Gestion de la Réserve Naturelle des îles Lavezzi" and the "Office de l'Environnement

de la Corse, Arrêté 93-149." This study is a personal program of the "Centre de Recherche sur la Biologie des Populations d'Oiseaux, Paris."

## LITERATURE CITED

- BARROWCLOUGH, G. F. 1978. Sampling bias in dispersal studies based on finite data. *Bird-Banding* 49:333-341.
- BATESON, P. 1983. Optimal outbreeding. Pages 257-277 in *Mate choice* (P. Bateson, Ed.). Cambridge University Press, Cambridge, United Kingdom.
- BENSCH, S., D. HASSELQUIST, AND T. VON SCHANTZ. 1994. Genetic similarity between parents predicts hatching failure: Nonincestuous inbreeding in the Great Reed Warbler? *Evolution* 48:317-326.
- BOLLINGER, E. K., S. J. STEVEN, AND G. W. BARRETT. 1993. Inbreeding avoidance increase dispersal movements of the meadow vole. *Ecology* 74:1153-1156.
- BORG, J., AND R. CACHIA-ZAMMIT. 1997. Philopatry of the Cory's Shearwater *Calonectris diomedea* on Malta. *II Merill* 28:23-25.
- BRETAGNOLLE, V., AND B. LEQUETTE. 1990. Structural variation in the call of the Cory's Shearwater (*Calonectris diomedea*, Aves, Procellariidae). *Ethology* 85:313-323.
- BRETAGNOLLE, V., AND J.-C. THIBAUT. 1995. Method for sexing fledglings in Cory's Shearwaters and comments on sex-ratio variation. *Auk* 112:785-710.
- COLEMAN, J. T., A. E. COLEMAN, AND D. ELPHICK. 1994. Incestuous breeding in the Mute Swan *Cygnus olor*. *Ring and Migration* 15:127-128.
- CRAIG, J. L., AND I. G. JAMIESON. 1988. Incestuous mating in a communal bird: A family affair. *American Naturalist* 131:58-70.
- GIBBS, H. L., AND P. R. GRANT. 1989. Inbreeding in Darwin's Medium Ground Finches (*Geospiza fortis*). *Evolution* 43:1273-1284.
- GRANADEIRO, J. P. 1993. Variations in measurements of Cory's Shearwater between populations and sexing by discriminant analysis. *Ring and Migration* 14:103-112.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140-1162.
- GREENWOOD, P. J. 1989. Inbreeding, philopatry and optimal outbreeding in birds. Pages 207-223 in *Avian genetics* (F. Cooke and P. A. Buckley, Eds.). Academic Press, London.
- GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1-21.
- GREENWOOD, P. J., P. H. HARVEY, AND C. M. PERRINS. 1978. Inbreeding and dispersal in the Great Tit. *Nature* 271:52-54.
- HOOGLAND, J. L. 1992. Levels of inbreeding among prairie dogs. *American Naturalist* 139:591-602.
- LAMBIN, X. 1994. Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles (*Microtus townsendii*). *Ecology* 75:224-235.
- MASSA, B., AND M. LO VALVO. 1986. Biometrical and biological considerations on the Cory's Shearwater. Pages 293-313 in *Mediterranean marine avifauna* (X. Monbailliu, Ed.). Springer-Verlag, Berlin.
- MAYR, E. 1963. *Animal species and evolution*. Harvard University Press, Cambridge, Massachusetts.
- MOUGIN, J.-L., B. DESPIN, C. JOUANIN, AND F. ROUX. 1987. La fidélité au partenaire et au nid chez le Puffin cendré, *Calonectris diomedea borealis*, de l'île Selvagem Grande. *Le Gerfaut* 77:353-369.
- PUSEY, A., AND M. WOLF. 1996. Inbreeding avoidance in animals. *Trends in Ecology and Evolution* 11:201-206.
- RALLS, K., P. H. HARVEY, AND A. M. LYLES. 1986. Inbreeding in natural populations of birds and mammals. Pages 35-36 in *Conservation biology: The Science of scarcity and diversity* (M. Soulé, Ed.). Sinauer Associates, Sunderland, Massachusetts.
- RANDI, E., F. SPINA, AND B. MASSA. 1989. Genetic variability in Cory's Shearwater (*Calonectris diomedea*). *Auk* 106:411-417.
- RICHDALE, L. E. 1957. *A population study of penguins*. Clarendon Press, Oxford.
- RISTOW, D., F. FELDMANN, W. SCHARLAU, AND M. WINK. 1990. Population structure, philopatry and mortality of Cory's Shearwater *Calonectris diomedea diomedea*. *Die Vogelwelt* 111:172-181.
- RISTOW, D., AND M. WINK. 1980. Sexual dimorphism of Cory's Shearwater. *II Merill* 21:9-12.
- SAS INSTITUTE, INC. 1994. *SAS/STAT user's guide*, version 6, 4th ed. SAS Institute, Inc., Cary, North Carolina.
- SHIELDS, W. M. 1983. Optimal inbreeding and the evolution of philopatry. Pages 132-159 in *The ecology of the animal movement* (I. R. Swingland and P. J. Greenwood, Eds.). Clarendon Press, Oxford.
- SWATSCHEK, I., D. RISTOW, AND M. WINK. 1994. Mate fidelity and parentage in Cory's Shearwater *Calonectris diomedea*—Field studies and DNA fingerprinting. *Molecular Ecology* 3:259-262.
- THIBAUT, J.-C. 1993. Natal philopatry in the Cory's Shearwater (*Calonectris diomedea diomedea*) on Lavezzi Islands, Corsica. *Colonial Waterbirds* 16:77-82.
- THIBAUT, J.-C. 1994. Nest-site tenacity and mate fi-

- delity in relation to breeding success in Cory's Shearwater *Calonectris diomedea*. *Bird Study* 41: 25–28.
- WINK, M., P. HEIDRICH, U. KAHL, AND I. SWATSCHKE. 1993. Inter- and intraspecific variation of the nucleotide sequence of the cytochrome *b* gene in Cory's Shearwater (*Calonectris diomedea*), Manx Shearwater (*Puffinus puffinus*) and the Fulmar (*Fulmarus glacialis*). *Zeitschrift Naturforschorschung* 48:504–509.
- WOLFF, J. O. 1993. What is the role of adults in mammalian juvenile dispersal? *Oikos* 68:173–176.
- WOOLLER, R. D., J. S. BRADLEY, AND J. P. CROXALL. 1992. Long-term population studies of seabirds. *Trends in Ecology and Evolution* 7:111–114.

Received 28 January 1997, accepted 11 August 1997.

Associate Editor: R. M. Zink

*The Auk* 115(2):486–489, 1998

## Chipmunks Use Leverage to Eat Oversized Eggs: Support for the Use of Quail Eggs in Artificial Nest Studies

DAVID P. CRAIG<sup>1</sup>

*Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado 80309, USA*

Several authors have questioned the use of Japanese Quail (*Coturnix japonica*) eggs as bait in artificial nests (Roper 1992, Haskell 1995a, DeGraaf and Maier 1996, Major and Kendal 1996). Based on observations at a feeding station, Haskell (1995a) concluded that the gape of eastern chipmunks (*Tamias striatus*) was not sufficiently wide to open quail eggs. Consequently, Haskell (1995a,b) questioned the validity of studies that use quail eggs in artificial nests to evaluate the relationship between nest predation and forest fragmentation. In this paper, I focus on the behavior of least chipmunks (*Tamias minimus*) eating quail eggs in artificial nests in the Colorado Front Range. Observations of other sciurids also are described to add to the general understanding of rodent predation behavior (Callahan 1993). I also comment on possible biases in Haskell's (1995a) observations of chipmunk egg predation and the weak support of his critical view of quail-egg experiments (1995b). Finally, I suggest a protocol for evaluating a potential predator's ability to consume eggs.

**Methods.**—I used two sources of data. First, 10 predation events by sciurids were observed without a blind during the summers of 1993 to 1996 in the foothills of Boulder County, Colorado. Observations were collected opportunistically from artificial nests as part of a broader study of nest predation by corvids (Craig 1997). Artificial nests resembling nests of American Robins (*Turdus migratorius*) were constructed from mud, grass, and a wicker basket and

placed 1 to 2 m above the ground in conifers. Each nest had a fine-grass lining, one or two *Coturnix* quail eggs, and a color-matched plasticene egg (hereafter "clay" egg) wired to the nest. Predators often were startled during observations, and I never observed the initial attack on artificial nests.

Second, I observed predator behavior during the entire predation event from a blind by staging predation events in July and August of 1995. An artificial nest (with one clay egg and two quail eggs) was placed on a porch rail 3 m from a platform feeder that was visited frequently by a variety of birds, least chipmunks, and fox squirrels (*Sciurus niger*). A total of 15 separately constructed nests (30 quail eggs and 15 clay eggs) was used. Nests were placed on the porch railing repeatedly and were not independent of each other. This may have facilitated habituation by the predators to the nests and eggs. Nevertheless, Steller's Jays (*Cyanocitta stelleri*) and Black-billed Magpies (*Pica pica*) regularly nested in the study area (pers. obs.), and their eggs are about the same size and shape as quail eggs (Harrison 1979).

**Results.**—During four years of opportunistic observations, I observed chipmunks (*T. minimus* and *T. quadrivittatus*) eating eggs from artificial nests three times. Twice the chipmunks were recorded eating an egg in the nest and once on the ground directly below the nest. It is possible that the egg on the ground fell out of the nest, broke open, and then was consumed. Nevertheless, in all three cases the egg was opened through its small end. During the same period, one golden-mantled ground squirrel (*Spermoph-*

<sup>1</sup> E-mail: dcraig@columbia-center.org