

Short notes

VARIATIONS IN NEST MORTALITY IN THE EUROPEAN STORM PETREL *HYDROBATES PELAGICUS*

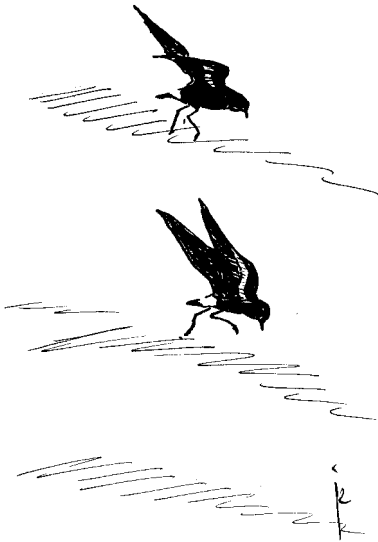
EDUARDO MÍNGUEZ^{1,2} & DANIEL ORO^{3*}

Mínguez E. & D. Oro 2003. Variations in nest mortality in the European Storm Petrel *Hydrobates pelagicus*. *Ardea* 91(1): 113-117.

Procellariiformes breed mainly on inaccessible islands and many species nest underground reducing egg or chick losses caused by predation. Nevertheless, Procellariiformes show low reproductive rates. In a four years study of breeding European Storm Petrel, we estimated nest mortality for three stages: incubation, brooding and chick-rearing period, using the Mayfield-40% 's method. The highest value of daily nesting mortality was found during the brooding period (after incubation). Furthermore, daily egg failure varied less between years than daily chick mortality rate, both in the brooding and the chick-rearing stages. These results are in accordance with theoretical differences in both the duration of foraging trips of parents, and daily nest energy requirements among the three stages.

Key words: *Hydrobates pelagicus* - breeding success - food limitation - nest mortality - seabirds - Mediterranean - energetic constraints

¹Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), J. Gutiérrez Abascal 2, E-28006 Madrid, Spain. ²Universidad Miguel Hernández, Dpto. de Biología Aplicada, Avenida del Ferrocarril s/n, E-03202 Elche, Alicante, Spain; *Corresponding author*: ³Instituto Mediterráneo de Estudios Avanzados IMEDEA (CSIC-UIB), Miquel Marqués 21, 07190 Esporles (Mallorca), Spain; E-mail: d.oro@uib.es



Nest mortality is one of the major selective factors determining the reproductive strategies of birds (e.g. Ricklefs 1969, 1993; Martin 1995). Nest predation and food limitation are the primary sources of nesting mortality (Ricklefs 1969; Martin 1995 and references therein). Among seabirds, Procellariiformes nest predominately in burrows on inaccessible islands, and therefore relatively few eggs and chicks are lost to predators (Ricklefs 1969; Warham 1990, 1996). Thus, reproductive failure in seabirds should vary mainly in relation to food resources (Monaghan *et al.* 1992), or fluctuations in energy demands during the nesting period (Ricklefs 1969). Balancing this view of seabird reproduction based on food limitation, Ricklefs (1983) proposed that limitation may not be due to the quality of the food resource itself,

but rather to the problem of transporting food between the feeding area and the nest site. The energy required at the nest generates demand for food gathering that must be satisfied during the time devoted by parents to forage. This time is less during incubation and brooding stages, with only one parent foraging at a time, than is during the chick rearing stage, when Procellariiformes are no longer tied to the nest, except briefly to feed the chick, and, if needed, devote all their time to forage (Ricklefs 1983, 1990). However, during the brooding stage, parents must to feed and to warm the hatchling, being energy demands at the nest higher than during the incubation period. Under such circumstances, one may predict that in pelagic seabirds breeding failure might be highest during the brooding period and lowest

Table 1. Daily mortality rates with 95% confidence limits and mean percent nest mortality for Storm Petrels breeding in Benidorm Island during 1993-96. Mean losses for different periods and nesting failure were calculated using daily survival rates in each phase and local data on incubation period and brooding stage. The chick-rearing period was considered only until day 40 after hatching because during the last days chicks become highly mobile.

Year	1993	1994	1995	1996	Total
No. of nests	133	122	75	161	491
<i>Incubation period</i>					
Nests/nest-d/failed nests	133/3268.9/53	122/3916.8/46	75/1880.4/34	161/5404.4/63	491/14471/196
Daily mortality	0.0162 ± 0.0022	0.0117 ± 0.0034	0.0181 ± 0.0031	0.0117 ± 0.0015	0.0135 ± 0.0010
Nest mortality (%)	48.00	37.66	51.80	37.44	42.04
<i>Brooding period</i>					
Nests/nest-d/failed nests	13/68/1	27/96.4/6	4/15.4/2	23/116.6/3	67/296.4/12
Daily mortality	0.0147 ± 0.0146	0.0622 ± 0.0246	0.1299 ± 0.0857	0.0257 ± 0.0147	0.0405 ± 0.0114
Nest mortality (%)	10.65	38.64	65.26	17.97	26.95
<i>Chick-rearing period</i>					
Nests/nest-d/failed nests	79/2545.6/3	70/2222.6/14	39/1226.8/1	95/2843.2/12	283/8838.2/30
Daily mortality	0.0012 ± 0.0007	0.0063 ± 0.0017	0.0008 ± 0.0008	0.0042 ± 0.0012	0.0034 ± 0.0006
Nest mortality (%)	3.75	18.51	2.61	12.81	10.43
<i>Nestling period</i>					
Nest mortality (%)	14.00	50.00	66.17	28.48	34.57

during the chick-rearing period. We tested this hypothesis by comparing the daily nest mortality during the three nesting stages with theoretically different energy requirements for reproduction (incubation, brooding, and chick-rearing periods) in the European Storm Petrel *Hydrobates pelagicus*, a pelagic bird with very low predation at the nests (Mínguez 1994).

Field work was carried out at Benidorm Island (38°30'N, 0°08'E), Mediterranean coast of Spain, from 1993 to 1996. The study areas are two high density colonies inside caves, where petrels nest under boulders and in crevices (Mínguez 1994). Every year, marked nests were checked throughout all stages of the nesting period (mean time lag in 1993: 9 ± 5.03 d, range 1-17, $n = 14$ visits; 1994: 2.16 ± 2.41 d, range 1-12, $n = 54$ visits; 1995: 7.26 ± 9.05 d, range 1-28, $n = 16$ visits; 1996: 6.33 ± 5.45 d, range 1-20, $n = 22$ visits).

Intervals between checking were longer on the onset (i.e. middle April) and on the end (middle August) of the breeding season, but shorter (usually daily), during the hatching period, in order to estimate the daily rate of chick loss during the short brooding period. Nest checking did not cause any of the observed patterns of losses through disturbance (authors, unpubl. data). The only predators of petrels are the Yellow-legged Gulls *Larus michahellis** breeding on the island (Mínguez 1994). As eggs usually are not removed from the nest by parents, egg failure was noted as eggs which remained in the nest unattended between two visits or more. When egg desertion or chick death occurred between two visits, the disappearance was assigned to 2/5 of the interval (Mayfield 1975). Mayfield 40% 's method (Mayfield 1961, 1975), as modified by Johnson (1979) and Hensler & Nichols (1981), was used to esti-

**Larus michahellis*, previously known as *Larus cachinnans michahellis*

mate daily mortality rate at nests. Survival was estimated for three periods (incubation, brooding, chick-rearing period) with expected different energy demand. The calculation of variance and of differences between survival rates was based on the formulae of Hensler & Nichols (1981). The level of significance chosen was $P = 0.05$. Mean incubation period (the number of days between laying and hatching) was considered to be 40 days (Davis 1957; Mínguez 1998). The nestling period includes the 'brooding period', in which one parent is always present at the nest covering its chick, and the 'chick-rearing period', in which the chick is alone at least during daylight. In Benidorm, the brooding period lasts 7.6 ± 1.84 days, (range 5 - 11, $n = 24$, authors, unpubl. data). We considered chicks to have fledged if they were at least 40 days old when last observed, because older chicks become highly mobile within crevices and are difficult to find during daylight. Thus, to estimate chick mortality during the chick-rearing period, the duration of this stage was set at 32.4 days (i.e. the recorded nestling stage minus the brooding period). We excluded from the analyses 8 nests destroyed by disturbance caused by fledglings of Yellow-legged Gull in 1993 (Mínguez 1994) and 12 nests destroyed by a large wave in 1995 (Mínguez 1998).

There were no differences between laying dates of pairs that succeeded in raising their chick and those that did not (for 1994, laying date of unsuccessful nests = 24.96 ± 11.82 , $n = 46$, laying date of successful nests = 24.66 ± 14.56 , $n = 61$, t

= 0.12, $P = 0.90$; 19 April = day 1 of the first laying in the colony). This suggests that the risk of predation seems to be approximately constant during the petrel breeding season. Yearly differences between daily mortality rates for the brooding and incubation stages or during the chick-rearing stage were significant only in 1994 (Tables 1 and 2). However, when pooling data across years, daily nest mortality was higher during the brooding period than during the chick-rearing period and incubation period (Tables 1 and 2). Furthermore, the lowest daily mortality occurred during the chick-rearing stage. Daily mortality rates were higher during the incubation period than during the nestling period (i.e. mortality during brooding and chick-rearing stages pooled) every year except in 1993 (Table 2). Daily egg failure varied less between years ($CV = 22.46\%$) than daily chick mortality, both compared with the brooding stage ($CV = 89.42\%$, F -test using the squares of CV : $F_{3,3} = 15.84$, $P = 0.024$) or the chick-rearing period ($CV = 83.33\%$, $F_{3,3} = 13.76$, $P = 0.029$). However, yearly variability did not differ significantly between the brooding and the chick-rearing period ($F_{3,3} = 0.87$, $P = 0.54$). Breeding success in birds depends on factors such as egg quality (e.g., egg fertility, egg composition), or parental quality (e.g., incubation behaviour, foraging ability, cooperation between male and female, persistence in adverse conditions), which are directly related with energy constraints (e.g. Ricklefs 1969). However, stochastic events related to nest quality,

Table 2. Z values of the Hensler & Nicholson test (1981) used to compare daily nest mortality of Storm Petrels breeding in Benidorm for different periods. Mortality rates are shown in Table 1. (* $Z > 1.96$, i.e. $P < 0.05$).

Year	Incubation versus nestling period	Incubation versus brooding period	Incubation versus chick-rearing period	Brooding versus chick-rearing period
1993	0.1051	0.1021	6.5051*	0.9257
1994	10.2390*	2.0472*	2.2651*	2.2682*
1995	11.2030*	1.3042	5.4314*	1.5065
1996	5.2683*	0.9550	3.9140*	1.4619
Total	12.873*	2.3450*	8.8817*	3.2352*

such as unseasoned cold or heat, flooding or predation, may affect nesting success in Procellariiformes (e.g. Wooller *et al.* 1992).

A greater mortality during the early chick stage has been described in other studies of European Storm Petrels (Davis 1957; Scott 1970; Cadiou 2001). This pattern could be explained if the chick-brooding period imposes maximum energy demands on adults or/and the chick would be most vulnerable when neglected at this stage. Other explanations could be that chick mortality might also be affected by the weight at hatching, determined by the egg-size (Weidinger 1997) or by ectoparasite load (Merino *et al.* 1999). In Benidorm Island, chick survival was lowest during the brooding period and increased sharply as the chicks grew. This, together with the existence of a long laying period (Mínguez 1994), suggests that factors other than differences in food availability during the breeding stages may account for the differences in mortality of Storm Petrel chicks. The high yearly variability in survival of Storm Petrel chicks during the nestling period also suggests that the amount of parental care (feeding and heating) to the chick would be constrained by food availability during the early stages of the nestling period, mainly the brooding stage.

This study is a contribution of the project 'Conservación de las aves marinas de las Islas Columbretes y los Islotos de Benidorm' in agreement with *Conselleria de Medi Ambient de la Generalitat Valenciana*, as an action of the LIFE project 'Conservación de las ZEPAs insulares de la Comunidad Valenciana' (contract B4-3200/98/447). We thank José P. Veiga, J.M. Aparicio, A. Martínez-Abraín, J.J. Sanz, J. Viñuela, Mark Bolton, John C. Coulson, J. S. Sedinger, D.W. Anderson and especially Bob Ricklefs for constructive comments on the manuscript. Field study has been partially supported to EM by a grant of *Conselleria de Medi Ambient de la Generalitat Valenciana* (DOGV 2483, 04.04.1995) and by the project PB94-0070-C02-01 of the *Dirección General de Investigación Científica y Técnica*. EM is indebted to Benidorm ferry's company for allowing him to travel to the island without any toll, and particularly grateful to Belén Belliure for her assistance in the field. This study is a part of a research granted by the award 'Premio Gonzalo Nárdiz de Etología y Ecología de la Fauna -1997-'.

Cadiou B. 2001. The breeding biology of the European Storm-petrel *Hydrobates pelagicus* in Brittany, France. *Atl. Seabirds* 3: 149-164.

- Davis P. 1957. The breeding of the Storm Petrel. *Br. Birds* 50: 85-101.
- Hensler G.L. & J.D. Nichols 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation analysis. *Wilson Bull.* 93: 42-53.
- Johnson D.H. 1979. Estimating nest success: The Mayfield method and an alternative. *Auk* 96: 651-661.
- Martin T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Mon.* 65: 101-127.
- Mayfield H.F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255-261.
- Mayfield H.F. 1975. Suggestion for calculating nest success. *Wilson Bull.* 87: 456-466.
- Merino S., Mínguez E. & B. Belliure 1999. Ectoparasites effects on nestling Storm Petrels. *Waterbirds* 22: 297-301.
- Mínguez E. 1994. Censo, cronología de puesta y éxito reproductor del Paíño común (*Hydrobates pelagicus*) en la isla de Benidorm (Alicante, E de España). *Ardeola* 4: 1-9.
- Mínguez E. 1998. The costs of incubation in the British Storm-Petrel: An experimental study in a single-egg layer. *J. Avian Biol.* 29: 183-189.
- Monaghan P., J.D. Uttley & M.D. Burns 1992. Effect of changes in food availability on reproductive effort in Arctic Terns *Sterna paradisaea*. *Ardea* 80: 71-81.
- Ricklefs R.E. 1969. An analysis of nesting mortality in birds. *Smiths. Contr. Zool.* 9: 1-48.
- Ricklefs R.E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Stud. Avian Biol.* 8: 84-94.
- Ricklefs R.E. 1990. Seabird life histories and the marine environment: some speculations. *Col. Waterbirds* 13: 1-6.
- Ricklefs R.E. 1993. Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. *Current Orn.* 11: 199-276.
- Scott D.A. 1970. The breeding biology of the Storm Petrel. PhD-thesis, Univ. of Oxford, Oxford.
- Weidinger K. 1997. Variations in growth of Cape Petrel *Daption capense* chicks. *J. Zool (Lond)* 242: 193-207.
- Warham J. 1990. The petrels. *Acad. Press*, London.
- Warham J. 1996. The behaviour, population biology and physiology of the petrels. *Acad. Press*, London.
- Wooller R.D., J.S. Bradley & J.P. Croxall 1992. Long-term population studies of seabirds. *TREE* 7: 111-114.

Veel stormvogelachtigen broeden op afgelegen eilandjes of andere voor predatoren moeilijk bereikbare plaatsen. Veel soorten broeden ook nog eens in holen onder de grond om zo de verliezen van eieren en kuikens beperkt te houden. Ondanks deze aanpassing is het broedsucces van stormvogelachtigen in de regel laag. In een vier jaar durende studie op het eiland Benidorm in de Middellandse Zee (38°30'NB, 00°08'OL) werd de sterfte van eieren en jongen van het Stormvogeltje *Hydrobates pelagicus* gevolgd volgens de Mayfield-40% methode. Drie stadia werden daarbij onderscheiden: het bebroeden van de eieren (*incubation*), de eerste fase van jongenzorg, waarbij altijd minstens een van

beide oudervogels in het nest aanwezig is (*brooding*), en de tweede fase van jongenzorg, wanneer het kuiken overdag alleen in het nest zit (*chick-rearing*). De enige predator van stormvogeltjes op Benidorm is de Geelpootmeeuw *Larus michahellis*. Het broedsucces van vogels hangt af van factoren zoals de kwaliteit van de eieren of de oudervogels. Beide factoren zijn gerelateerd aan energetische beperkingen, zoals het voedselaanbod. Daarnaast kunnen factoren die zijn gerelateerd aan de kwaliteit van het nest of de nestlocatie van belang zijn, waardoor voor het seizoen abnormale warmte of koude, overstromingen of predatie het broedsucces kunnen beïnvloeden. De sterfte onder

Stormvogeltjes op Benidorm bleek het hoogst in de eerste fase van jongenzorg, net nadat de eieren waren uitgekomen. Het verlies aan eieren verschilde van jaar tot jaar veel minder dan de sterfte onder kuikens in de twee fasen van de jongenzorg. Deze resultaten zijn in overeenstemming met de theoretische verschillen in zowel de duur van de voedselvluichten van de ouders tijdens de drie fasen van de reproductie als de dagelijkse voedselbehoefte van het jong in het nest tijdens de twee fasen van de jongenzorg. (CJC)

Received 27 November 2001, accepted 22 August 2002.
Corresponding editor: Kees (C.J.) Camphuysen

MOORHEN *GALLINULA CHLOROPUS* FEMALES LAY EGGS OF DIFFERENT SIZE AND β -CAROTENE CONTENT

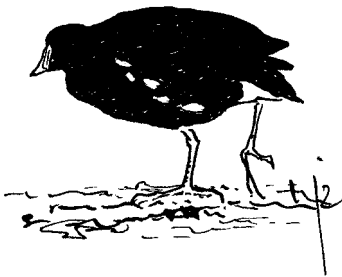
STEFANO FENOGLIO, MARCO CUCCO & GIORGIO MALACARNE

Fenoglio S., M. Cucco & G. Malacarne 2003. Moorhen females lay eggs of different size and β -carotene content. *Ardea* 91(1): 117-121

In birds, carotenoids deposited in the eggs can influence the progeny's prospects of survival. As a potentially limiting resource, carotenoids should be allocated optimally by the mother during egg production. The Moorhen *Gallinula chloropus* produces large clutches. We tested if females differ in their allocation of macronutrients (proteins and lipids) and the key micronutrient, β -carotene. To this end, we measured intra- and inter-clutch variability in egg size and contents. All parameters showed large inter-clutch differences and low intra-clutch variability. The total amount of β -carotene decreased in smaller eggs, indicating that females did not compensate for smaller egg size with a higher content of this micronutrient.

Key words: *Gallinula chloropus* – β -carotene – egg composition – inter-clutch variability.

Department of Sciences and Advanced Technologies, University of Eastern Piedmont, Via Cavour 84, 15100 Alessandria, Italy, E-mail: fenoglio@unipmn.it



There is increasing interest in the influence of maternal effects on the quality of offspring (Qvarnstrom & Price 2001). Since egg production is an energetically expensive process (Nager *et al.* 2001), maternal investment in egg size and composition can have a strong influence on offspring fitness (Williams 1994; Blomqvist *et al.* 1997).

Unequal resource allocation among eggs may be the optimal strategy for females with access to limited resources (Reed & Vleck 2001). It has long been known that each female can lay eggs of different size (Lack 1968) or relative amount of yolk and albumen (Carey 1996; Swennen & Van der Meer 1995) and with a different composition