Incubation capacity limits clutch size in south polar skuas

JEONG-HOON KIM[1]*, HYUN PARK[1], EUN JUNG CHOY[1], IN-YOUNG AHN[1] and JEONG-CHIL YOO[2]

[1]*Division of Polar Biology and Oceanography, Korea Polar Research Institute, Songdo-dong 7-50, Yeonsu-gu, Incheon 406-840, South Korea*
[2]*Korea Institute of Ornithology and Department of Biology, Kyung-Hee University, Seoul 130-701, South Korea*
jhkim94@kopri.re.kr

Abstract: The incubation-limitation hypothesis suggests that clutch size in some birds is limited by incubation capacity. However, this remains disputed amongst ornithologists. This study aimed to test whether incubation capacity limits the maximum clutch size to two eggs in south polar skuas (*Catharacta maccormicki* Saunders) by comparing the egg and nest temperatures as well as hatchability between two-egg and three-egg clutches. Although the vast majority of clutches contained one or two eggs, four naturally occurring three-egg clutches were found at Barton Peninsula, King George Island over three breeding seasons (2004–2005, 2005–2006 and 2006–2007). Regardless of clutch size, all incubating parents exhibited two discernible brood patches. The mean egg and nest temperatures of the three-egg clutches were significantly lower than were those of the two-egg clutches. The accumulated time that egg temperature decreased below 30°C in three-egg clutches was approximately eight times longer than that in two-egg clutches. The hatchability of natural one-egg (89.5%) and two-egg clutches (95.4%) were significantly higher than that of the three-egg clutches, which was zero. Our results suggest that the maximum clutch size in south polar skuas is probably restricted by incubation capacity.

Introduction

The factors that determine clutch size have been a topic of debate among ornithologists since Lack first hypothesized about the evolution of bird clutch size in 1947. Lack (1947) suggested that the clutch size of gulls and waders belonging to the Charadriiformes is limited by incubation capacity. In a cold environment, parents pay a high energetic cost for incubation, and these costs increase with clutch size (Thomson *et al*. 1998). When more eggs are laid, parents are forced to spend more time incubating (Sandercock 1997, Larsen *et al*. 2003, Niizuma *et al*. 2005) and probably cannot warm all eggs effectively (Reid *et al*. 2000, Niizuma *et al*. 2005). The incubation-limitation hypothesis has been both accepted and rejected with regard to the Charadriiformes. Specifically, it has not held true for some waders (Sandercock 1997, Arnold 1999, Wallander & Andersson 2002, Larsen *et al*. 2003), but experiments in gulls and skuas revealed that the hatching success rates of enlarged clutches were lower than those of normal sized clutches (see Andersson 1976, Niizuma *et al*. 2005).

Typically, egg temperature is maintained at *c*. 30–40°C during the incubation period but the thermal tolerance of embryos differs among bird species (see Webb's review 1987). When embryos are left at lower than optimal temperatures, their development is delayed (Booth 1987). If an embryo is left below 30°C for a long time, it may die or develop abnormally (Booth 1987, Székely *et al*. 1994, Engstrand & Bryant 2002). Niizuma *et al*. (2005) reported that a relatively low egg temperature and longer durations of egg temperatures below 30°C in enlarged clutches resulted in low hatchability in black-tailed gulls *Larus crassirostris* Vieillot.

The incubation capacity, or the effective heat transmission to the egg, is probably closely related to the number of brood patches in gulls. If a bird attempts to incubate more eggs than it has brood patches, hatchability may decrease. Skuas (*Stercorariidae*), which have two brood patches (Phillips 2002), generally lay two-eggs clutches (Andersson 1976, Furness 1987), and three-egg clutches have rarely been reported (Bonner 1964, Furness 1987, Millar *et al*. 1992, Phillips 2001, 2002). Indeed, with the exception of one case (Phillips 2002), hatching successes for natural or artificial supernormal clutches in skuas are relatively low (Andersson 1976, Furness 1987, Phillips 2001). Accordingly, we would expect that south polar skuas are not able to warm three eggs with two brood patches. We thus tested the incubation-limitation hypothesis in south polar skuas (*Catharacta maccormicki* Saunders) by comparing mean egg and nest temperatures and the total time that egg temperature dropped below 30°C between artificially created two-egg and three-egg clutches. In addition, to investigate the incubation efficiency, we estimated the hatching success and hatchability of natural two-egg and three-egg nests.

Methods

Study area

The study was conducted on the Barton Peninsula (62°13'S, 58°47'W) King George Island, South Shetland Islands during the summers (November–February) of 2004–2009. The area of the snow (or ice) free zone that is available for nesting on the Barton Peninsula is c. 8.4 km² (Kim et al. 2005). Two skua species, south polar skuas and brown skuas (Catharacta lonnbergi Matthews) and their mixed pairs, breed at the study site, with the south polar skua being the predominant species (Kim et al. 2005).

Clutch size, number of brood patches and mating patterns

To locate nests, we searched around breeding sites and observed the territorial behaviour of south polar skuas throughout five consecutive breeding seasons (2004–2009). Once the first egg was observed in the nest, we visited that nest daily with the exception of blizzard days until egg laying was complete. The maximum egg number in a nest was defined as the clutch size. To identify the sex, the number of brood patches and mating pattern of breeding pairs, 36 pairs (13, 21 and 2 pairs having one, two and three-egg clutches, respectively) and 12 incubating adults (just one adult of a pair) of south polar skuas were caught. All skuas caught were sexed on the basis of the Z and W-linked CHD genes from blood samples (Fridolfsson & Ellegren 2000) and banded with one KOPRI (Korea Polar Research Institute) numbered steel leg ring. To check whether three-egg clutches were created by polygyny or by female-female pairing in south polar skuas, we attempted to identify the mating pattern of owners having three eggs on the basis of individual sexing data. This, however, was not possible for two of the four three-egg clutches because one three-egg clutch found in 2006 was predated in the early stages of incubation, and the other clutch was found after the nest was abandoned in late January 2005, which was too late to determine the mating pattern.

Egg and nest temperature

To compare the incubating egg temperature between normal (one- and two-egg) and three-egg clutches in south polar skuas, we measured the egg temperature (T_{egg}) using dummy eggs during 2008–2009. In a recent study performed by Niizuma et al. (2005), dummy eggs were made for measuring T_{egg} by filling natural eggshells with agarose gel. However, it is difficult to collect natural skua eggs for experiments because researchers must minimize their disturbance when working in the Antarctic region. Although addled eggs were sometimes collected after incubation had finished, shells of addled eggs poorly preserved, and the number of addled eggs was insufficient for the experiment. Thus, we used the eggshells of domestic

geese whose size (c. 85 x 60 mm) was slightly larger than that of the south polar skua (c. 70 x 50 mm, J.-H. Kim, unpublished data). The goose eggs were adjusted to the size of a south polar skua egg using following methods: first, parts of the narrow and broad ends of the goose eggs were cut off to a width of 5 cm, then we paired the shell ends such that they had a total length of 7 cm. The dummy eggs were then filled with agarose gel (see Niizuma et al. 2005), and a datalogger (ACR Systems INC., SmartButton, DG1921; 17.35 diameter x 5.89 mm height) was loaded into the centre. Dataloggers were calibrated in a thermal bath (10–50°C) measured using a mercury thermometer before loading in the dummy eggs. Dummy eggs were painted to match the natural colour of south polar skua eggs after sealing.

Five clutches of two eggs were selected for measuring egg and nest temperatures, after testing for the acceptance of the dummy egg and enlarged clutch size by incubating adults. To evaluate whether T_{egg} and nest temperature (T_{nest}) are influenced by incubating one additional egg, we measured the temperatures of two-egg and three-egg clutches in the same nests. T_{nest} was measured simultaneously with T_{egg} using a similar datalogger. To measure the T_{nest} we placed a datalogger at a 1 cm depth inside the nest cup. Data loggers in dummy eggs and nests recorded the T_{egg} and T_{nest} every minute for 24 hours. The skuas' own eggs were incubated in an incubator in the King Sejong Station during the experiments and returned to their original nest once the work was finished.

To evaluate the incubation equality for each egg within a nest, we calculated the difference between the lowest and highest T_{egg} (ΔT_{egg}). Embryos of many seabirds cannot maintain normal development below 30°C (Dawson 1984). We determined the total amount of time that T_{egg} dropped below 30°C over a day to compare the disturbance time of an embryo's development between two-egg and three-egg clutches.

Hatching success and hatchability

To investigate the hatching success and hatchability of south polar skuas, we visited 60, 91 and 86 nests every day with the exception of blizzard days during 2004–2005, 2005–2006 and 2006–2007, respectively. Hatching success was estimated as the percentage of hatched eggs per nest. If we found an unhatched egg during the normal hatching time, we determined whether the egg was addled. An egg was defined as addled if it made a gurgling sound when shaken. If eggs disappeared during the laying and incubation periods, we regarded them as predated eggs because the main causes of egg loss at this site are predation by brown and south polar skuas (c. 95% of eggs lost; J.-H. Kim, unpublished data). The hatchability per nest is defined here as the percent of hatched eggs from the remaining eggs in a nest during the normal hatching time. Thus, predated eggs were excluded for estimating the hatchability.

Table I. Frequency distribution of clutch size of south polar skuas (2004–2009).

Years	No. of clutches (%)		
	one-egg	two-egg	three-egg
2004–05	14 (24.1)	43 (74.1)	1 (1.7)
2005–06	20 (20.0)	79 (77.0)	1 (1.0)
2006–07	19 (22.9)	62 (74.7)	2 (2.4)
2007–08	16 (64.0)	9 (36.0)	0 (0)
2008–09	16 (50.0)	16 (50.0)	0 (0)
Pooled	85 (28.5)	209 (70.1)	4 (1.3)

Statistical analyses

All statistical analyses were performed using SPSS ver. 12.0. To avoid pseudoreplication (see Hulbert 1984), we used T_{egg}, ΔT_{egg}, and T_{nest} measured every 10 min (144 measurements per day) for statistical analyses. Meanwhile, we accumulated the time that T_{egg} dropped below 30°C during the 24 hours for 1440 measurements per egg. A Mann-Whiney U-test was done to detect differences in T_{egg}, ΔT_{egg}, and T_{nest} between two- and three-egg clutches. The differences in T_{egg} within a nest were analysed using a t-test for two-egg clutches and a one-way ANOVA for three-egg. We compared the hatching success and hatchability between one-egg and two-egg clutches using a Mann-Whitney U-test. In this comparison, the hatching success and hatchability of three-egg clutches was excluded because no hatched eggs were present in the three-egg clutches.

Results and discussion

Clutch size

Although both one-egg and two-egg clutches were common, the majority of clutches contained two eggs in 2004–2005, 2005–2006, and 2006–2007 but not in 2007–2008 and 2008–2009 (Table I). We also found four naturally occurring three-egg clutches over the 2004–2007 study periods (Table I). Generally, supernormal clutches have been regarded as outcomes of polygyny (Conover et al. 1979, Kovacs & Ryder 1983), egg retrieval behaviour (Shugart 1980, Kim et al. 2006), brood parasitism (Conover et al. 1979), or female-female pairing (Hunt & Hunt 1977, Conover et al. 1979, Shugart 1980, Conover 1983, Kovacs & Ryder 1983). However, the probability that three-egg clutches were formed by brood parasitism or egg retrieval behaviour is low because south polar skuas are very aggressive towards intruders and defend their breeding territory intensively during the breeding season. In addition, neighbouring nests are probably located too far apart to draw a neighbour's eggs into one's own nest (see Kim et al. 2005). Bonner (1964) and Phillips (2002) observed that polygynous parents produce three-egg clutches in brown skuas. However, we did not observe three different adults at a nest containing three eggs. Not only all skua pairs with
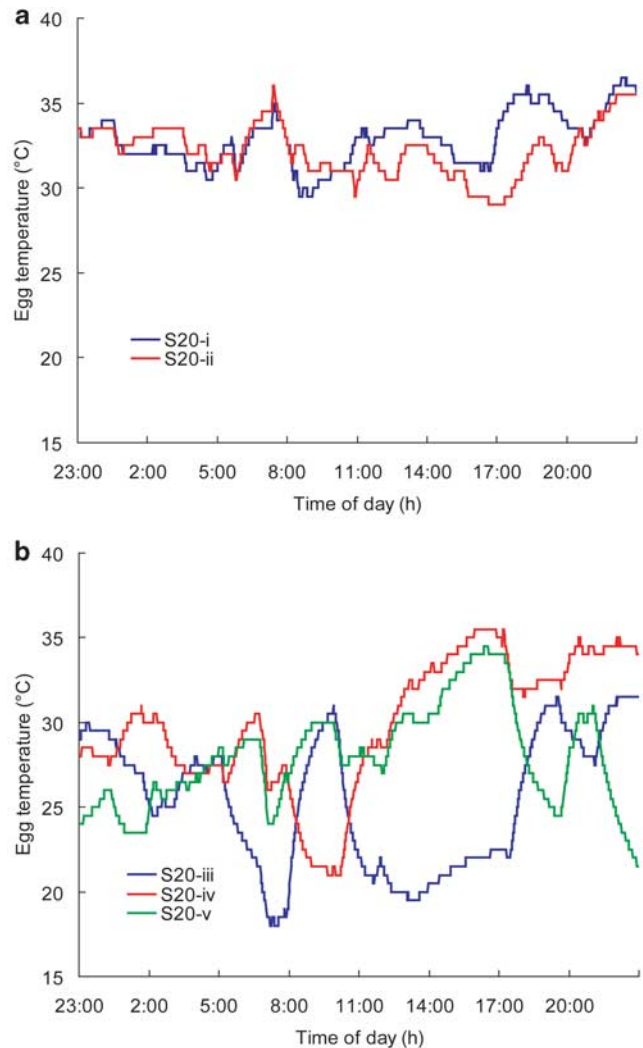

Fig. 1. An example of egg temperatures (T_{egg}) measured during one day (1440 min) in two-egg and three-egg clutches of south polar skuas. Data of T_{egg} are from the nest S20. **a.** Two-egg clutch, **b.** three-egg clutch.

one-egg and two-egg clutch but also two of the four pairs with three-egg clutches were heterosexual pairs. Nevertheless, the possibility that polygynous parents created the supernormal clutches cannot be ruled out because we could not identify the mating pattern for two of the owners of three-egg nests.

Table II. Mean egg temperature (T_{egg}), differences between lowest and highest temperatures (ΔT_{egg}), nest temperature (T_{nest}), and accumulated time per egg that T_{egg} dropped below 30°C during the one-day measurements. Data presented are mean ± SD and sample sizes are given in parentheses.

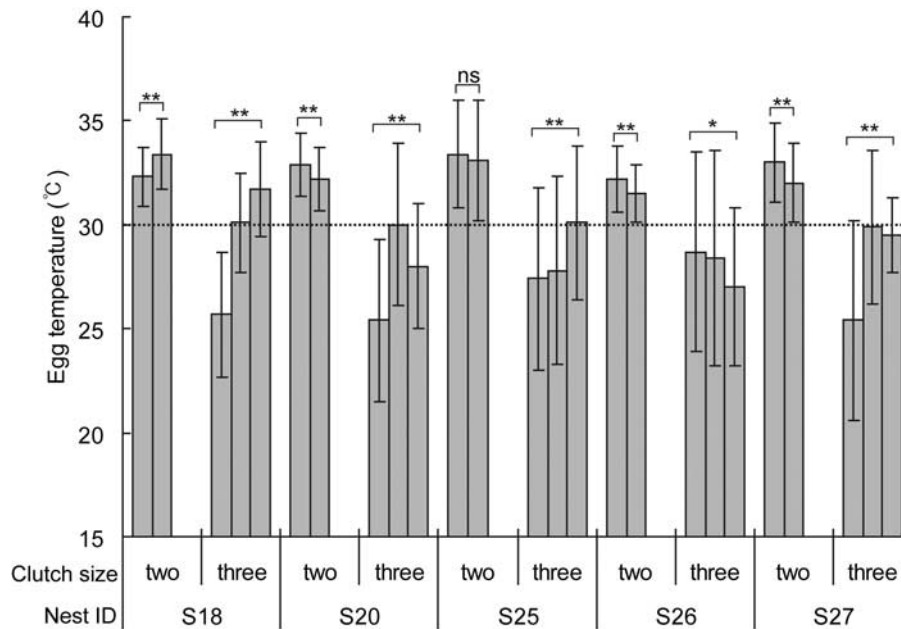|	Clutch size	
	two-egg	three-egg
Mean T_{egg} (°C)	32.6 ± 0.6 (10)	28.4 ± 1.9 (15)
ΔT_{egg} (°C)	1.6 ± 0.4 (5)	7.7 ± 0.6 (5)
Duration below 30°C (min)/egg	105.0 ± 59.1 (10)	811.3 ± 283.8 (15)
Mean T_{nest} (°C)	13.5 ± 0.2 (5)	12.3 ± 0.7 (5)

Fig. 2. Comparisons of individual egg temperatures (± SD) measured over one day within the nest for two-egg and three-egg clutches. Significant levels are symbolized by: *$P < 0.05$, **$P < 0.001$.

Incubation efficiency

As in other Stercorariidae, the incubating south polar skuas caught had two discernible brood patches regardless of clutch size. Incubation capacity is closely related to the number of brood patches. Niizuma *et al*. (2005) showed as an example that the number of brood patches in black-tailed gulls limits the number of incubated eggs in an enlarged clutch. Thus, when south polar skuas attempted to incubate three eggs, they could warm just two eggs with brood patches (Fig. 1).

Fluctuations in T_{egg} of two eggs of both clutches showed synchronous patterns within same period (Fig. 1). However, T_{egg} of the extra egg in three-egg clutches tended to change in opposition to the other two eggs, and the composition of the pair of eggs following the synchronous T_{egg} fluctuation pattern shifted randomly (Fig. 1b). The mean egg temperature (T_{egg}) of two-egg clutches was significantly higher than that of three-egg clutches ($z = 4.12$, $P < 0.001$), and the ΔT_{egg} values of two-egg clutches were significantly smaller than those of three-egg clutches ($z = 2.61$, $P < 0.01$; Table II). We also found significant differences in individual T_{egg} values within clutches in both clutch groups, except for one case in a two-egg clutch (Fig. 2). Even though we found significant differences in T_{egg} within the two-egg clutches, the overall mean T_{egg} for all eggs in these clutches did not fall below 30°C. In contrast, the mean temperatures of 12 eggs among the 15 eggs in the three-egg clutches were below 30°C. The mean accumulated time per egg that the T_{egg} dropped below 30°C in three-egg clutches was significantly longer than in the two-egg clutches ($z = 4.16$, $P < 0.001$; Table II). The above results indicate that parents could not efficiently incubate three eggs at a time.

We found that when one egg was added to a clutch with two eggs, the T_{nest} decreased significantly. The mean T_{nest} when skuas incubated two eggs was higher than that when they incubated three eggs ($z = 2.61$, $P < 0.01$; Table II). Szentirmai *et al*. (2005) demonstrated that the cooling rate of an egg is a function of the clutch size and ambient temperature. In our experiment one egg could not be covered with a brood patch and probably would sit in a gap between the nest and the body of the parent. Thus, the gap probably allows the nest to be exposed to the low ambient temperature, thereby decreasing the T_{egg}. Our results suggest that the incubation efficiencies could be reduced by decreasing the thermal insulation of the nest in the enlarged clutches.

Table III. Hatching success and hatchability of south polar skuas.

Year	Clutch size	Hatching success (%)[a]	n[b]	Hatchability (%)[c]	n[d]
2004–05	one-egg	44.4 ± 52.7	9	80.0 ± 44.7	5
	two-egg	55.7 ± 43.3	35	95.8 ± 14.1	24
	three-egg	0	1	0	1
2005–06	one-egg	50.0 ± 52.7	10	100	5
	two-egg	67.6 ± 42.2	51	94.9 ± 15.4	39
	three-egg	0	1	0	1
2006–07	one-egg	66.7 ± 49.2	12	88.9 ± 33.3	9
	two-egg	69.0 ± 39.7	42	95.6 ± 14.4	34
	three-egg	0	2	0	1
Pooled	one-egg	53.2 ± 42.7	31	89.5 ± 31.5	19
	two-egg	58.9 ± 45.3	128	95.4 ± 14.9	97
	three-egg	0	4	0	3

a = average hatching success (± SD) per nest, b = no. of nests, c = average hatchability (± SD) per nest obtained from eggs not predated during the normal hatching time, d = number of nests having at least one egg not predated during normal hatching time.

Hatching success and hatchability

No significant differences in hatching success were found between the one-egg and two-egg clutches (Table III). The relatively high hatchability (89.5% in one-egg clutches; 95.4% in two-egg clutches) in normal-sized clutches suggested that eggs were incubated efficiently. However, we found that the hatching success and hatchability of three-egg clutches were zero (Table III). Hatchability is decreased when eggs are exposed to below-normal incubation temperatures for long periods of time (Vleck & Vleck 1996, Niizuma *et al.* 2005). Even though the embryos of some seabirds can endure and survive at low temperatures (e.g. 26°C for Adélie penguins (*Pygoscelis adeliae* (Hombron & Jacquinot); Weinrich & Baker 1978), 10°C for fork-tailed storm-petrels (*Oeanodroma furcata* (Gmelin); Vleck & Kenagy 1980), 10°C for western gulls (*Larus occidentalis* Audubon; Bennett *et al.* 1981), and 5°C for Heermann's gulls (*Larus heermanni* Cassin; Bennett & Dawson 1979)), it remains unknown how long seabird embryos can sustain cooler temperatures, and most cannot maintain normal development below 30°C (Dawson 1984). In our study, the mean accumulated time per egg that the T_{egg} dropped below 30°C over the entire incubation period (*c.* 30 days; J.-H. Kim, unpublished data) was *c.* 406 hours for three-egg clutches (range 128–626 hours) compared to *c.* 53 hours for the two-egg clutches (range 7–87 hours). This suggests that relatively long exposures to below 30°C induced embryo mortality in three-egg clutches. Therefore, enlarged clutches are more at risk for cold temperature induced mortalities in the Antarctic region than are normal-sized clutches.

Conclusions

Our results indicate that the incubation efficiency of south polar skuas is negatively affected by incubating one additional egg. This low incubation efficiency prevented the successful hatching of abnormal, three-egg clutches, resulting in zero percentage hatchability in three-egg clutches. Thus, our data supports the incubation-limitation hypothesis for south polar skuas. Incubating an enlarged clutch imposes additional physiological costs to parents (e.g. Reid *et al.* 2000, Niizuma *et al.* 2005) and may affect parental survival (Reid *et al.* 2000). Given the tendency for birds to instinctively try to warm all eggs, they will probably incur more costs for incubating a larger clutch (Gabrielsen & Steen 1979). We did not estimate changes in the body conditions of parents incubating two-egg and three-egg clutches during the incubation period to evaluate parental costs. However, such an investigation should be conducted to test the trade-off hypothesis in south polar skuas.

References

ANDERSSON, M. 1976. Clutch size in the long-tailed skua *Stercorarius longicaudus*: some field experiments. *Ibis*, **118**, 586–588.

ARNOLD, T.W. 1999. What limits clutch size in waders? *Journal of Avian Biology*, **30**, 216–220.

BENNETT, A.F. & DAWSON, W.R. 1979. Physiological responses of embryonic Heermann's gulls to temperature. *Physiological Zoology*, **52**, 413–421.

BENNETT, A.F., DAWSON, W.R. & PUTNAM, R.W.P. 1981. The thermal environment and tolerance of embryonic western gulls. *Physiological Zoology*, **54**, 146–154.

BONNER, W.N. 1964. Polygyny and super-normal clutch size in the brown skua, *Catharacta skua lonnbergi* (Matthews). *British Antarctic Survey Bulletin*, No. 3, 41–47.

BOOTH, D.T. 1987. Effect of temperature on development of malleefowl *Leipoa ocellata* eggs. *Physiological Zoology*, **60**, 437–445.

CONOVER, M.R. 1983. Female-female pairings in Caspian terns. *Condor*, **55**, 346–349.

CONOVER, M.R., MILLER, D.E. & HUNT JR, G.L. 1979. Female-female pairings and other unusual reproductive associations in ring-billed and California gulls. *Auk*, **96**, 6–9.

DAWSON, W.R. 1984. Metabolic responses of embryonic seabirds to temperature. *In* WHITTOW, G.C. & RAHN, H., *eds. Seabird energetics*. New York: Plenum Press, 139–157.

ENGSTRAND, S.M. & BRYANT, D.M. 2002. A trade-off between clutch size and incubation efficiency in the barn swallow *Hirundo rustica*. *Functional Ecology*, **16**, 782–791.

FRIDOLFSSON, A.K. & ELLEGREN, H. 2000. Molecular evolution of the avian CHD1 genes in the Z and W sex chromosomes. *Genetics*, **155**, 1903–1912.

FURNESS, R.W. 1987. *The skuas*. London: A. & C. Black, 363 pp.

GABRIELSEN, G. & STEEN, J.B. 1979. Tachycardia during egg-hypothermia in incubating ptarmigan (*Lagopus lagopus*). *Acta Physiologica Scandinavica*, **107**, 273–277.

HUNT JR, G.L. & HUNT, M.W. 1977. Female-female pairing in western gulls (*Larus occidentalis*) in Southern California. *Science*, **7**, 1466–1467.

HULBERT, S.T. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

KIM, J.-H., NAM, H.-K., FULTON, G.R. & YOO, J.-C. 2006. Egg retrieval as a source of nests with supernormal and mixed egg clutch in little terns *Sterna albifrons*. *Journal of Ecology and Field Biology*, **29**, 545–550.

KIM, J.-H., CHUNG, H., KIM, J.H., YOO, J.-C. & AHN, I.-Y. 2005. Nest distribution of skuas on Barton and Weaver peninsulas of King George Island, the Antarctic. *Ocean and Polar Research*, **27**, 443–450.

KOVACS, K.M. & RYDER, J.P. 1983. Reproductive performance of female-female pairs and polygynous trios of ring-billed gulls. *Auk*, **100**, 658–669.

LACK, D. 1947. The significance of clutch size. *Ibis*, **89**, 302–352.

LARSEN, V.A., LISLEVAND, T. & BYRKJEDAL, I. 2003. Is clutch size limited by incubation ability in northern lapwings? *Journal of Animal Ecology*, **72**, 784–792.

MILLAR, C.D., LAMBERT, D.M., BELLAMY, A.R., STAPLETON, P.M. & YOUNG, E.C. 1992. Sex-specific restriction fragments and sex ratios revealed by DNA fingerprinting in the brown skua. *Journal of Heredity*, **83**, 350–355.

NIIZUMA, Y., TAKAGI, M., SENDA, M., CHOCHI, M. & WATANUKI, Y. 2005. Incubation capacity limits maximum clutch size in black-tailed gulls *Larus crassirostris*. *Journal of Avian Biology*, **36**, 421–427.

PHILLIPS, R.A. 2001. *Stercorarius parasiticus* Arctic skua. *Birds of the Western Palearctic Update*, **3**, 25–41.

PHILLIPS, R.A. 2002. Trios of brown skuas at Bird Island, South Georgia: incidence and composition. *Condor*, **104**, 694–697.

REID, J.M., MONAGHAN, P. & RUXTON, G.D. 2000. The consequences of clutch size for incubation conditions and hatching success in starlings. *Functional Ecology*, **14**, 560–565.

SANDERCOCK, B.K. 1997. Incubation capacity and clutch size determination in two calidrine sandpipers: a test of the four-egg threshold. *Oecologia*, **110**, 50–59.

SHUGART, G.W. 1980. Frequency and distribution of polygyny in Great Lakes herring gulls in 1978. *Condor*, **82**, 426–429.

SZÉKELY, T., KARSAI, I. & WILLIAMS, T.D. 1994. Determination of clutch-size in the Kentish plover *Charadrius alexandrinus*. *Ibis*, **136**, 341–348.

SZENTIRMAI, I., SZÉKELY, T. & LIKER, A. 2005. The influence of nest size on heat loss of penduline tit eggs. *Acta Zoologica Academiae Scientiarum Hungaricae*, **51**, 59–66.

THOMSON, D.L., MONAGHAN, P. & FURNESS, R.W. 1998. The demands of incubation and avian clutch size. *Biological Reviews*, **73**, 293–304.

VLECK, C.M. & KENAGY, G.J. 1980. Embryonic metabolism of the fork-tailed storm petrel: physiological patterns during prolonged and interrupted incubation. *Physiological Zoology*, **53**, 32–42.

VLECK, C.M. & VLECK, D. 1996. Embryonic energetics. *In* CAREY, C., ed. *Avian energetics and nutritional ecology*. New York: Chapman & Hall, 550–554.

WALLANDER, J. & ANDERSSON, M. 2002. Clutch size limitation in waders: experimental test in redshank *Tringa totanus*. *Oecologia*, **130**, 391–395.

WEBB, D.R. 1987. Thermal tolerance of avian embryos: a review. *The Condor*, **98**, 874–898.

WEINRICH, J.A. & BAKER, J.R. 1978. Adélie penguin (*Pygoscelis adeliae*) embryonic development at different temperatures. *Auk*, **95**, 569–576.