J Ornithol (2010) 151:765–770
DOI 10.1007/s10336-010-0508-x

ORIGINAL ARTICLE

Egg survival is related to the colour matching of eggs to nest background in Black-tailed Gulls

Who-Seung Lee · Young-Soo Kwon · Jeong-Chil Yoo

Received: 16 May 2009 / Revised: 8 January 2010 / Accepted: 25 February 2010 / Published online: 19 March 2010

Abstract A long-standing hypothesis posits that, for species with exposed nests, a close match between the colour of the eggs and that of the nest in which they are laid should enhance egg survival, but this has rarely been tested in a rigorous manner. Here, we demonstrate the effects of egg–nest colour matching on egg survival in Black-tailed Gulls (*Larus crassirostris*) on Hongdo Island, Korea. We quantified the ground colour of eggshells and that of the nest background using a digital camera and computerized RGB and greyscale colour systems. We show that a close match of eggshell ground colour and nest background colour was associated with increased chances of eggs surviving through to hatching. In particular, there were strong survival advantages for eggs matching the nest colour in sites with poor concealment, whereas there was no effect of eggshell ground colour in nests that were more concealed by vegetation. Our findings support the hypothesis that egg colour functions to make eggs cryptic and that egg colouration may be a significant factor affecting egg loss.

Keywords Colour quantification · Camouflage · Eggshell colour · Hatching success · Nest site characteristic

Communicated by P. H. Becker.

W.-S. Lee · Y.-S. Kwon · J.-C. Yoo (✉)
Department of Biology and The Korea Institute of Ornithology, Kyung Hee University, Seoul 130-701, South Korea
e-mail: jcyoo@khu.ac.kr

W.-S. Lee (✉)
Division of Ecology and Evolutionary Biology, Faculty of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK
e-mail: whoseung@gmail.com

Present Address:
Y.-S. Kwon
Korea National Park, National Park Research Institute, 16-1, Hogyeong-ri, Jucheon-myeon, Namwon-si, Jeollabuk-do 590-811, South Korea

Introduction

Traditionally avian egg colouration has been explained as a result of natural selection to reduce predation (for review, see Underwood and Sealy 2002). Tinbergen et al. (1962) hypothesised that egg colour and egg-spot pattern in gulls had evolved to camouflage eggs from predators since eggs appeared to blend with their nest background. During the incubation period, the concealment of eggs could directly influence the survival of eggs (Burger and Gochfeld 1988) since the major cause of nest failure at the egg stage is usually identified as predation (Ricklefs 1969; Furness and Monaghan 1987).

Most studies of nest site characteristics (Burger and Gochfeld 1988; Jones 2001; Lee et al. 2006a) are typically concerned with the influence of environmental factors, but rarely test whether there is an interaction between the characteristics of the nest and of the egg in determining breeding success (e.g. Hockey 1982; Lloyd et al. 2000). The match of eggs to their background is likely to be especially important in ground-nesting species in which, in the absence of the incubating parent, the nest and its contents are exposed to predators. Several authors (e.g. Lack 1968; Tinbergen et al. 1962; Nguyen et al. 2003) have suggested that the protective colour and spots of eggs in gulls and shorebirds could affect egg survival. For instance, Nguyen et al. (2003) showed that the cryptic colour and spots of eggs in Semipalmated Plovers (*Charadrius* *semipalmatus*) could make eggs less conspicuous. While egg-spots can be evaluated by comparing patterns, typical methods for the quantification of colour are complicated by the fact that colours change with illumination, and that different observers often perceive colour differently.

Villafuerte and Negro (1998) and Blanco and Bertellotti (2002) suggested a method for quantifying colour using a digital camera and computer system, in which colour was measured in terms of the colour index-values of the RGB (red, green, and blue) and greyscale (black and white). Using mean values of RGB of each photographed egg, quantification of eggshell ground colour is possible (Blanco and Bertellotti 2002). These methods have proved especially useful in various studies of the influence of egg colour on breeding biology, such as the influence of egg colour polymorphism on egg survival (Blanco and Bertellotti 2002), egg colour and sexual selection (Moreno and Osorno 2003), and egg colour and colony site tenacity (Sánchez et al. 2004). However, they have not been used in studies of the conspicuousness of eggs to predators. We utilised this approach to examine the influence of the degree of colour match between eggs and the nest background on hatching success (=egg survival) in the Black-tailed Gull (*Larus crassirostris*), a ground-nesting species that is known to manipulate the visual appearance of nest sites to reduce the risk of predation (Lee et al. 2006a, b).

Methods

Study species and area

The Black-tailed Gull, one of the commonest seabirds in Korea, typically has a clutch size of two or three eggs (Lee et al. 2005). The background colour of the eggs ranges from light greenish to dark brown, and is overlaid with spots of dark brown to black (Won 1981). In most two-egg clutches, the eggs are of similar colouration. While variation (e.g. different colour or shade) can arise in a small number of clutches (especially those of more than 3 eggs), the proportion of such large clutches is low (mean clutch size is 1.89 ± 0.59; Kwon 2004). In this study, there were only 14 nests (15%) with over three eggs and also the colour of third eggs was not different from first and second eggs. It is not clear why the egg colour variation is greater in larger clutches, but Kwon (2004) reported that one cause might be intra-specific brood parasitism. Hongdo Island (34°31′87″N, 128°43′88″E) holds the largest and densest breeding colony of Black-tailed Gulls in Korea, and the breeding density on the island has been increasing according to recent census data (8.4 ± 2.8 nests per 25 m^2 in 2003 and 16.3 ± 5.3 nests per 25 m^2 in 2008; Lee et al. 2008a). The island is located about 50.5 km from the mainland. The area of the island is 98,380 m^2, the highest point is about 115 m above sea level, and cliffs with a slope of over 45° surround the coastline. The sedge *Carex boottiana,* which is used as the most common nesting material to build the nest cup, covers the whole island except the rocky cliffs (Lee et al. 2006a). During the study, there was only one breeding species, Black-tailed Gulls, on the island, plus one pair of Peregrine Falcons (*Falco peregrinus*). Known predators of eggs and chicks of Black-tailed Gulls on Hongdo Island include conspecific adults, Peregrine Falcons and the wild cat (*Felis catus*) (Lee et al. 2005), but the most common predators are conspecific adults.

Hatching success

The study was conducted during the breeding season (April–August) of 2003. While it is possible to define two distinct breeding areas on the island (rocky-cliff area and grassy area), the hatching success during the study was similar between areas (Lee et al. 2008b). However, to exclude nest location effects in the current analysis, the data were only obtained from nests in the grassy area (=colony centre); we also excluded nests in which some eggs were addled and died at hatching. We recorded the fate of eggs in 93 nests by daily monitoring of nests and recording the number of eggs present and hatched eggs until at least 15 days after the expected hatching date of eggs having the same laying date (Lee et al. 2008b). We recorded the causes and number of eggs that disappeared from the nest or failed to hatch, and calculated hatching success in each clutch as hatched eggs divided by laid eggs.

Nest site characteristics

In previous studies (Lee et al. 2006a, b), we found that vegetation cover and nest wall positively influenced breeding success in Black-tailed Gulls. In order to examine Tinbergen's hypothesis, we examined whether the degree of concealment of the nest site from predators influenced the degree of egg crypsis. Vegetation cover was defined as the percentage of vegetation (in contrast to bare ground) present in the zone within about 0.5 m of the centre of the nest, and the percentage of the nest circumference (=nest wall) that was ringed by a wall of concealing material (rock or vegetation), providing some cover to the nest or restricting its visibility from above. We directly measured vegetation cover (50.3 ± 3.1%) and nest-wall (60.2 ± 2.3%) at the time of clutch completion (22.3 ± 0.4 days; 1 = 1 April) (Table 1). The detailed descriptions on the characteristics data were reported in Lee et al. (2006a).

Table 1 The colour plasticity of eggshell and nest background between RGB and greyscale system and measured nest site characteristics (vegetation cover and nest wall) ($n = 93$ nests) of Black-tailed Gull (*Larus crassirostris*)

	Mean	Min	Max
Colour plasticity			
Eggshell background			
RGB	134.6 ± 1.2	104.7	167.0
Greyscale	135.3 ± 1.5	98.3	156.9
Nest background			
RGB	131.5 ± 1.1	105.7	170.0
Greyscale	132.3 ± 1.4	101.0	167.0
Nest site characteristics			
Vegetation cover (%)	50.3 ± 3.1	0	100
Nest-wall (%)	60.2 ± 2.3	0	100

Quantification of colour match between eggs and nests

On 30 April 2003, we photographed each entire nest and clutch from above at a height of approximately 30 cm using a digital camera (Nikon-Coolpix 995, 1,280 × 960 pixels and resolution, and 256^3 colours). Pictures were photographed in natural lighting conditions with no shadow, and by the same person. The photographs were analysed using Adobe Photoshop CS2 software (Adobe System 2005). We randomly selected three 10 × 10 pixel samples (2.6 ± 0.1 cm^2, approximate 5% of egg surface) from the eggshell background of each egg and from the sedge vegetation making up each nest within about 0.5 m of the nest centre (=nest background) to obtain values in the RGB (red, green, and blue) and greyscale (black and white) using the info tool in Adobe Photoshop (Blanco and Bertellotti 2002; Nguyen et al. 2003). Mean values of RGB and greyscale were calculated for each clutch and nest (Westmoreland and Kiltie 1996; Blanco and Bertellotti 2002). While varying ambient light levels (due to changing weather or time of day) can change the values obtained for RGB scores, this was not a problem in the present study since we were comparing the relative difference in colour between eggshell ground and nest background on the same photograph. We concentrated on the ground colour of the eggs since the spotty pattern is relatively simple and varies rather little, and it is the match between the egg ground colour and the nest background that determines egg conspicuousness.

Statistical analysis

We compared the variation in colour of eggshell and nest background using *t* tests. To examine the effect of eggshell colour on hatching success, the difference between eggs and nest in the quantified colour values (using either RGB colour or greyscale systems), together with the extent of the vegetation cover and nest wall, were used as candidate independent variables in logistic regressions with hatching "success (1)" or "failure (0)" as the dependent variable (SPSS 2006), with 0 being coded if at least one egg in the nest was lost prior to hatching. The effect of colour matching between eggshell coloration and nest ground on hatching success was analysed in both colour systems using logistic regression models (LRM) with colour value, nest wall and vegetation cover as fixed effects and all interactions among variables. Logistic functions were obtained after sequentially removing the non-significant effects starting from the least significant interaction terms. Interactions were reported only if they were significant ($P < 0.05$). All means are presented with standard errors. This study was performed under the permission from the Cultural Heritage Administration of Korea, but all experiments on Hongdo Island were not permitted because of the protection of breeding population in Black-tailed Gulls for 10 years.

Results

The eggshell colour in complete clutches ($n = 93$ nests) was similar to the nest background colour, whether measured on the RGB scale (*t* test, $t = 1.922$, $P = 0.056$, $df = 184$) or the greyscale system ($t = 1.491$, $P = 0.138$, $df = 184$) (Table 1). Eggs were lost during the incubation period through both predation and disappearance (excluding some causes of egg loss in sample data; see

Table 2 Parameter estimates from logistic regression models predicting hatching success (1 = success with no egg loss) and (0 = failure with at least one egg loss) from the degree of colour match between eggs and nest background ('colour') and the extent of the wall surrounding the nest ('nest wall'; see "Methods" for details)

Factors	β	Wald	P
RGB			
Colour	−0.633	8.333	0.004
Nest wall	−0.074	4.560	0.033
Colour × Nest wall	0.010	7.314	0.007
Constant	6.758	8.561	0.003
Greyscale			
Colour	−0.756	8.792	0.003
Nest wall	−0.065	4.185	0.041
Colour × Nest wall	0.012	8.070	0.005
Constant	6.176	8.237	0.004

The analysis was done separately for the RGB and greyscale measures of colour. Significant parameters were estimated after sequentially removing the non-significant effects starting from the least significant interaction terms

"Methods"). The percentage of clutches in which at least one egg loss was recorded was 54.8% and the mean hatching success was 62.4 ± 4.0%. However, the probability of a nest having at least one egg disappear was strongly and positively related to the difference in colour between the eggshell and the nest, whether measured in terms of the RGB colour system or using the greyscale method (Table 2). There was also an independent positive effect of the extent of nest wall on hatching success (Table 2), whereas the influence of vegetation cover was not significant (Wald $\chi^2_1 = 0.590$, $P = 0.442$). There was also an interaction on hatching success between the colour match and the extent of the nest wall in both RGB and greyscale systems (Table 2). Thus, there was a high probability of hatching success (=the entire clutch surviving) when there was a close match of the colour of the eggshell and nest background even if there was little or no nest wall—conversely, the colour match had little effect when the nest was extensively shielded by a nest wall (Fig. 1). The probability of hatching when there was a close matching of the colour of the eggshell and nest background and fully screened nest-wall (=100% nest-wall) was unexpectedly low, but this may have been due to a small sample size (6 nests).

Discussion

Previous researchers (Collias and Collias 1984; Underwood and Sealy 2002) have discussed whether egg colour has evolved in response to the requirement for camouflage to reduce egg predation. Our results clearly show that hatching success is greatest when eggshell ground colour blends closely with nest background colour (Fig. 1). The cryptic colour of the eggs of the Black-tailed gull might prevent predators detecting them. By painting the natural shell of the Ostrich (*Struthio camelus*) a dark brown, Bertram and Burger (1981) found that the Ostrich was able to reduce egg predation because the surrounding ground colour is usually dark. Kilner (2006) reports that the advantage of eggs blending in with the colour of the nest background depends on the predators: such defences are more effective against avian predators than mammalian, because the latter tend to use odour cues to detect nest sites.

It would be expected that eggs that do not match the nest colour would have a higher chance of surviving in nest sites that are concealed from predators. We found that this was indeed the case. There was no effect of eggshell and nest colour matching on hatching success in nests with an extensive nest wall: egg survival in such nests was generally high irrespective of the contrast in colour between egg and nest. Perhaps surprisingly, this was not the case for

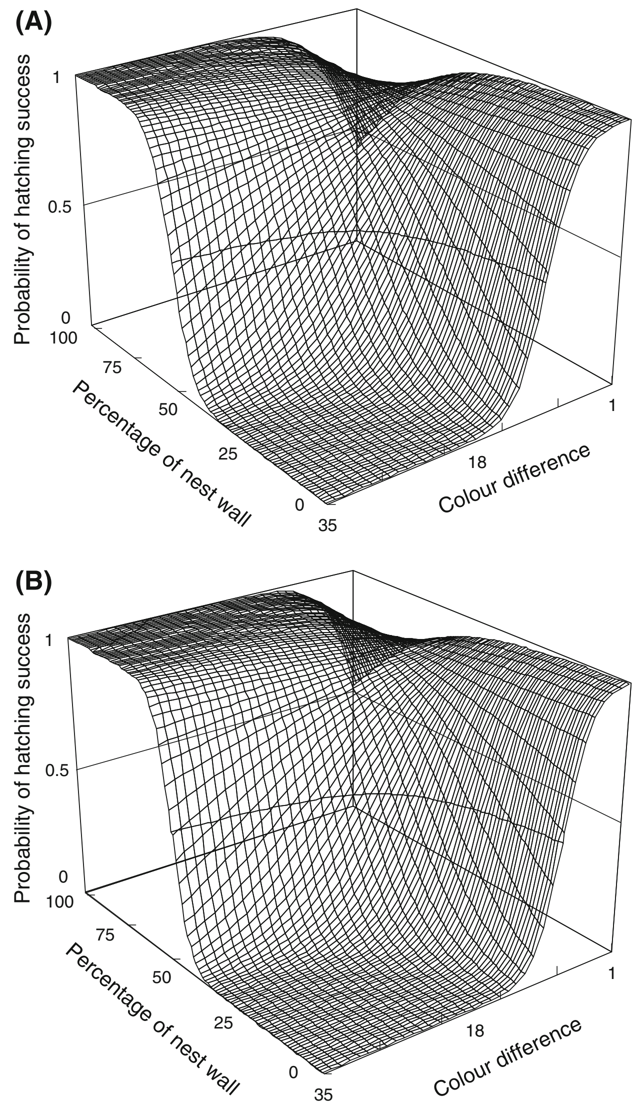

Fig. 1 Logistic regression of probability of hatching success (1 = success with no egg loss) and (0 = failure with at least one egg loss) in a Black-tailed Gull (*Larus crassirostris*) nest through to hatching in relation to the extent of the nest wall (% of nest circumference) and the degree of colour match between eggshell ground colour and nest background. Two different colour systems were used: (**a**) RGB and (**b**) Greyscale. Probabilities were calculated using the formula, Pr(egg survival) = $1/(1 + \alpha)$ where $\alpha = \exp(-6.758 + 0.663 \times$ colour difference $+ 0.074 \times$ nest wall $- 0.010 \times$ colour difference $\times$ nest wall) (**a**) and $\alpha = \exp(-6.176 + 0.756 \times$ colour difference $+ 0.065 \times$ nest wall $- 0.012 \times$ colour difference $\times$ nest wall) (**b**)

nests with vegetation cover, and therefore not providing much concealment since the high density in colonial birds such as the Black-tailed Gull might allow predators (=conspecific adults) to easily access neighbour nests, and so the defending efficiency of vegetation cover might be reduced. As can be seen in Fig. 1, however, it is unclear why the predicted probability of egg survival decreases in high extent of nest wall combined with a close matching of egg and nest colour (=in the upper corner). We can only presume that this effect was due to random effects and the small sample size.

Parents of higher quality and greater breeding experience should select nest sites with specific physical factors that are associated with higher breeding success (Lack 1968; Cezilly and Quenette 1988), such as a nest-wall in our case. Thus, the closeness of colour matching between the eggshell ground and nest background may reflect the quality and experience of parents. Sánchez et al. (2004) showed that a match of colour between egg and nesting substrate in Gull-billed Terns (*Gelochelidon nilotica*) is related to the fidelity of parents to a colony. Colony fidelity induces the process of adaptive selection of egg colours that better match the nesting substrate since parents have prior information on substrate colour in the colony. Particularly physiological condition of female before laying and breeding experience may affect the degree of colour matching between eggshell (as condition) and nests (as experience). Hongdo Island has two major habitat types with different consequences for breeding gulls: the rocky cliffs with higher clutch size and earlier laying date, and the grassy areas with lower clutch size and later laying date (Lee et al. 2008b). However, there was no difference between the two habitats in their degree of egg crypsis (unpublished data). In our study, it was not possible to tell whether the parents matched the colour of eggs and nest background by nest site selection or by changing the colour of eggs. Experimental work would be required to test these aspects. However the match of eggshell colour and nest-background colour is probably one of the defensive strategies selected by parents for higher survival of eggs.

In our study, we could not explore the function of the egg spots since egg spot patterns in Black-tailed Gull eggs are quite simple (Kwon 2004), unlike the various egg spot patterns in many other species (for example, Great tits, *Parus major*; Gosler et al. 2005). However, it is likely that egg spots also have specific functions to increase egg survival. For instance, contemporary military uniforms that have a pattern on a coloured background are thought to be better than older military uniforms that lack patterns, because the pattern improves the function of camouflage regardless of the closeness of match of the uniform base colour to the surrounding environment (Newark and Miler 2007).

Recently, behavioural studies using digital photographs and RGB scores (e.g. sexual ornamentation or camouflage) have been controversial because of the method of analysis (Stevens and Cuthill 2005; Stevens et al. 2007). The RGB values of photographs taken by digital camera can be converted to an objective real colour and also standard light and coloration (or greyscale standards) should be included in each photograph, since the RGB or greyscale values depend on location and light conditions (Cuthill I.C., personal communication). However, such standardised conditions are less important when comparing colour difference in a paired design as in the present study (i.e. nest and eggs are illuminated by the same light) because the results are internally consistent.

It has recently been shown that many birds can sense ultra-violet wavelengths (Cherry and Bennett 2001). Our study utilised RGB components from digital photos, but these did not provide information on colour matching in the UV range. It is important to assess the colour match with including the UV part of spectrum, particularly in such studies where the relevant predators are mostly birds (Håstad et al. 2005). In our study, however, the major predators are conspecific adults and so the effects of the colour matching on hatching success may indirectly be explained under visible wavelength (RGB and greyscale) because of the same condition between predator and prey. It is not known whether this species can see UV wavelengths, but it would be valuable to extend this study to include consideration of colours in the UV range. To summarise, our results support Tinbergen's hypothesis that a close match of colour between eggshell and nest background should decrease egg predation.

Zusammenfassung

Die Überlebenswahrscheinlichkeit von Gelegen der Japanmöwe *Larus crassirostris* hängt von der Farbanpassung an den Nestuntergrund ab

Seit langem besteht die Hypothese, dass bei Arten mit exponierten Neststandorten eine farbliche Übereinstimmung zwischen den Eiern und dem Nest, in das sie gelegt werden, das Überleben der Eier verbessern sollte, aber das wurde selten nach strengen Methoden geprüft. Hier zeigen wir die Auswirkung der Ei-Nest-Farbanpassung auf die Überlebenswahrscheinlichkeit der Eier der Japanmöwe (*Larus crassirostris*) auf Hongdo, Korea. Wir bestimmten die Grundfarbe der Eischalen und die des Nesthintergrunds mit einer Digital-Kamera und computerbasierten RGB- und Graustufen-Farbsystemen. Wir zeigen, dass eine gute Übereinstimmung zwischen der Grundfarbe der Eischale und der Farbe des Nesthintergrunds mit einer höheren Überlebenswahrscheinlichkeit der Eier bis zum Schlupf zusammenhing. Speziell an wenig versteckten Neststandorten bestanden für Eier, die gut an die Nestfarbe angepasst waren, hohe Überlebensvorteile, wohingegen für Nester an Standorten mit stärkerem Schutz durch Vegetation die Eischalen-Grundfarbe keinen Effekt hatte. Unsere Ergebnisse unterstützen die Hypothese, dass die Eifarbe dazu dient, die Eier zu verbergen, und dass die Eifärbung

ein wesentlicher, den Eiverlust beeinflussender Faktor sein könnte.

Acknowledgments We thank Dong-Won Kim and In-Ki Kwon for assistance in the field on Hongdo Island. We are grateful to Neil B. Metcalfe who contributed valuable suggestions to improve the manuscript and the translation of the manuscript. Special thanks are extended to Young Seuk Park, Marc Mangel, and Pat Monaghan for providing helpful comments on earlier drafts of the manuscript. We also thank Dr. Peter H. Becker (the subject editor) and two anonymous referees who provided constructive comments on the manuscript.

References

Adobe Systems (2005) Adobe Photoshop CS2. Seattle, Washington

Bertram BCR, Burger AE (1981) Are ostrich (*Struthio camelus*) eggs the wrong colour? Ibis 123:207–210

Blanco G, Bertellotti M (2002) Differential predation by mammals and birds: implications for egg-colour polymorphism in a nomadic breeding seabird. Biol J Linn Soc Lond 75:137–146

Burger J, Gochfeld M (1988) Nest-site selection by roseate terns in two tropical colonies on Culebra, Puerto-Rico. Condor 90:843–851

Cezilly F, Quenette PY (1988) Role des ecrans naturels attenant au nid chez le Goeland leucophee (*Larus cachinaans michahellis*). Alauda 56:41–50

Cherry MI, Bennett ATD (2001) Egg colour matching in an African cuckoo, as revealed by ultraviolet-visible reflectance spectrophotometry. Proc R Soc Lond B 268:565–571

Collias NE, Collias EC (1984) Nest building and bird behaviour. Princeton University Press, Princeton

Furness RW, Monaghan P (1987) Seabird ecology. Blackie, Glasgow

Gosler AG, Higham JP, Reynolds SJ (2005) Why are birds' eggs speckled. Ecol Lett 8:1105–1113

Håstad O, Victorsson J, Ödeen A (2005) Differences in color vision make passerines less conspicuous in the eyes of their predators. Proc Natl Acad Sci USA 102:6391–6394

Hockey PAR (1982) Adaptiveness of nest site selection and egg coloration in the African black oystercatcher *Haematopus moquini*. Behav Ecol Sociobiol 11:117–123

Jones J (2001) Habitat selection studies in avian ecology: a critical review. Auk 118:557–562

Kilner RM (2006) The evolution of egg colour and patterning in birds. Biol Rev Camb Philos Soc 81:383–406

Kwon YS (2004) Some aspects of the breeding biology of the black-tailed gull (*Larus crassirostris*). Dissertation, Kyung Hee University, Korea

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Lee WS, Kwon YS, Yoo JC (2005) Status of the breeding population of black-tailed gulls on Hongdo Island, Korea. Pac Seabirds 32:2–3

Lee WS, Kwon YS, Yoo JC, Song MY, Chon TS (2006a) Multivariate analysis and self-organizing mapping applied to analysis of nest-site selection in black-tailed gulls. Ecol Model 193:602–614

Lee WS, Kwon YS, Park YS, Chon TS, Yoo JC (2006b) Evaluation of environmental factors to predict breeding success of black-tailed gulls. Ecol Inf 1:331–339

Lee HS, Lee KS, Lee SW, Kim IK, Yang H, Kang TH, Song MJ, Yoo SH, Lee HH, Cho HJ, Yoo YM (2008a) Research of conservation and management of seabirds on uninhabited island designated as natural monument. National Research Institute of Cultural Heritage, Seoul, Korea

Lee WS, Kwon YS, Yoo JC (2008b) Habitat selection by black-tailed gulls on Hongdo Island, Korea. Waterbirds 31:495–501

Lloyd P, Plagányi É, Lepage D, Little RM, Crowe TM (2000) Nest-site selection, egg pigmentation and clutch predation in the ground-nesting Namaqua sandgrouse *Pterocles namaqua*. Ibis 142:123–131

Moreno J, Osorno JL (2003) Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? Ecol Lett 6:803–806

Newark T, Miler J (2007) Camouflage. Thames and Hudson, London

Nguyen LP, Nol E, Abraham KF (2003) Nest success and habitat selection of the semipalmated plover on Akimiski Island, Nunavut. Wilson Bull 115:285–291

Ricklefs RE (1969) An analysis of nesting mortality in birds. Smithson Contrib Zool 9:1–48

Sánchez JM, Corbacho C, del Viejo AM, Parejo D (2004) Colony-site tenacity and egg colour crypsis in the gull-billed tern. Waterbirds 27:21–30

SPSS (2006) SPSS for Windows, Rel. 15.0, Chicago

Stevens M, Cuthill IC (2005) The unsuitability of html-based colour charts for estimating animal colours—a comment on Berggren and Merilä (2004). Front Zool 2:1–14

Stevens M, Párraga CA, Cuthill IC, Partridge JC, Troscianko T (2007) Using digital photography to study animal coloration. Biol J Linn Soc 90:211–237

Tinbergen N, Broekhuysen GJ, Feekes F, Houghton JCW, Kruuk H, Szulc E (1962) Egg shell removal by the black-headed gull, *Larus ridibundus* L.; a behaviour component of camouflage. Behaviour 19:74–117

Underwood TJ, Sealy SG (2002) Adaptive significance of egg colouration. In: Deeming DC (ed) Avian incubation, behaviour, environment and evolution. Oxford University Press, Oxford, pp 280–298

Villafuerte R, Negro JJ (1998) Digital imaging for colour measurement in ecological research. Ecol Lett 1:151–154

Westmoreland D, Kiltie RA (1996) Egg crypsis and clutch survival in three species of blackbirds (Icteridae). Biol J Linn Soc 58:159–172

Won PO (1981) Illustrated flora and fauna of Korea. Avifauna, vol 25. Department of Education, Seoul, Republic of Korea