Common Ringed Plover eggs are well camouflaged in highly differing environments – a study on perception

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ABSTRACT

Common Ringed Plovers *Charadrius hiaticula* generally nest in open areas, quite often on light colored beaches, but in Iceland on dark colored volcanic substrates. We studied if their clutches are well camouflaged under those diverging conditions by (1) looking for associations between properties of clutches and nest sites, (2) measuring color differences between clutches and nest sites, and (3) measuring detectability for human subjects of clutches and nests in manipulated images. Properties of clutches were not associated with those of nest sites. Moreover, color differences between clutches and nest sites were substantial in Iceland, showing that – at least in this population – crypsis is not common, contrary to plovers that breed on light colored sea shores. However, we argue that camouflage of Common Ringed Plover clutches is mainly caused by disruptive coloration of the eggs and by selection and possibly adaptation of the nest habitat by the bird (by carrying light colored objects to the nest site, such as shell fragments and lichens). Detectability varied considerably between environments, but not between clutches, with clutches being best hidden in heterogeneous environments. Taken together, our results suggest that disruptive coloration of the clutch likely generates some level of crypsis, even on dark colored substrates.

Keywords

Common Ringed Plover, *Charadrius hiaticula*, Iceland, clutch, camouflage, crypsis, disruptive coloration, habitat selection, habitat adaptation, image manipulation

Short title:

Camouflage in highly differing environments

INTRODUCTION

Many animals, especially those that live in open areas, are vulnerable to predators. For them, their nests and young, it is a matter of life and death to be well camouflaged, i.e. almost undetectable to other animals (e.g. Stevens & Merilaita 2011). The same goes for the predators themselves, as their successes depend on detectability by their prey. It has been shown that visual detection of an object (or animal) can be thwarted by at least two phenomena, (1) close resemblance with the surroundings (*crypsis*: e.g. Cuthill et al. 2005, Endler 2006; with the classical example of the peppered moth *Biston betularia*: e.g. Majerus 1998) and (2) disruption of its outline by specific colors and patterns (*disruptive coloration*: e.g. Cuthill et al. 2005, Endler 2006, Schaefer & Stobbe 2006, Stevens et al. 2006).

Waders are particularly suited to investigate (nest and egg) camouflage, as many of these species do not conceal their nest. The effectiveness of camouflage of nests follows from the risk of being detected and robbed by a predator. It takes a lot of effort to measure this, but in plovers a few attempts have been made. For instance, Colwell et al. (2011) were able to associate habitat choice of Western Snowy Plovers *Charadrius alexandrines* with nest survival, and also with detectability of the nest by human observers. However, Nguyen et al. (2007), who measured survival of natural and – in more detail – artificial Semipalmated Plover *Charadrius semipalmatus* nests, failed to find associations with characteristics that were thought to affect camouflage. Similarly, Stoddard et al. (2016) could not establish associations between nest survival and such characteristics in Snowy Plovers *Charadrius nivosus*. Nonetheless, in various studies, the degree of matching between clutch and background was proposed as the major measure of camouflage (Nguyen et al. 2007, Lee et al. 2010, Amat et al. 2012, Gómez et al. 2016, Stoddard et al. 2016). In particular, color matching was considered to be an important determinant for camouflage. Thus, the analysis of color differences in digital photos of clutches and their immediate backgrounds was one of the main methods in these studies.

Common Ringed Plovers *Charadrius hiaticula* usually nest on bare or sparsely vegetated sandy or stony substrates close to the sea (Prater 1974, Glutz et al. 1975, Cramp & Simmons 1983, Pienkowski 1984, Wallander & Andersson 2003). Usually, the nest site differs from its immediate surroundings. It is a slight recession in the soil furnished with some, or quite a lot of small objects: shell fragments, little stones, pieces of lichens, seaweed or other plants. Most often, such objects are available in the surroundings of the nest site, but at lower densities. Apparently, these objects have been collected by the birds and transported a few meters, possibly for camouflage. In many areas (e.g. The Netherlands, Britain and Germany) nesting occurs on nearly white or light colored sandy plains close to the sea, but on Iceland, where light colored substrates are virtually absent, most Common Ringed Plovers nest on nearly black volcanic substrates (e.g.Thorisson 2013). Yet, all nests in these highly different types of environment are hard to find for humans, and most nests probably also for egg predators, such as gulls and skuas. At least four different hypotheses may be proposed to explain why these nests are so well hidden to our eyes: (1) egg colors and patterns differ between nests placed upon light and dark colored substrates, resulting in *crypsis* in both kinds of environments (e.g. Lee et al. 2010), (2) certain properties of the eggs (possibly *disruptive coloration*) make them hard to find against many types of substrate (e.g. Schaefer & Stobbe 2006), (3) camouflage is due to certain local properties of the environments chosen and manipulated for nesting by the bird (e.g. Colwell et al. 2011, Lovell et al. 2013), and (4) camouflage is due to another kind of interaction than close resemblance between properties of eggs and environments. Our aim was to investigate these possibilities, by (1) examining possible associations between properties of the egg and the environment where it was laid, with (2) special attention to color differences between clutch and nest site, and (3) by measuring detectability by human observers when backgrounds and clutches were experimentally manipulated.

METHODS

Study area and recording technique

Study sites were chosen on the basis of information on breeding Common Ringed Plovers. Nests were detected by carefully watching the behavior of individual birds. In 2013 (14-24 Jun) 14 nests with eggs (typified as X-nests) were found in southwestern Iceland near Selfoss (63°56'N, 21°00' W), Eyrarbakki (63°51'N, 21°09' W), Stokkseyri (63°50'N, 21°03' W) and Garður (64°04'N, 22°38' W). In 2014 (22-23 May) two nests with eggs (typified as T-nests) were found in The Netherlands, on Terschelling, (53°25'N, 5°22' E) and (6-23 Jun) 61 nests with eggs (typified as Y-nests) in western Iceland around Borgarness (64°34'N, 21°54' W), Grundarfjörður (64°56'N, 23°16' W) and Ólavsvik (64°54'N, 23°43' W). All nests were photographed in a 'standard' way. For that, we placed a rectangular wooden frame (outer measurements 24×19×2 cm, inner frame size 11×11 cm) over the clutch. Inner frame size was suited to a clutch *in situ*. Frame height was about the same as egg height. The frame's ground color was middle grey. Each of three sides of the frame had a series of small panels showing a gradient of slightly differing colors (one series of eight shades of grey, one series of eight reddish brown shades and one series of four yellow shades). These reference colors, corresponding to colors in pictures of Common Ringed Plover eggs and nest sites, were selected from the Microsoft Office color palette. We used a camera with flash, fixed on a stand 30 cm straight above the eggs and recorded an image including clutch and the major parts of the frame with the three color gradients, all in focus (Fig. 1). In addition, we made two pictures of each nest without the frame and (mostly) without flash: one from 'nearby' (from about 50 cm, camera approximately 40° downwards) and one showing the 'environment' of the nest (from about 2 m, camera approximately 20° downwards). Date, time and GPS coordinates of all nests were recorded when they were found. We suspected that Common Ringed Plover nests could benefit from the protection of tern colonies. We, therefore, noted whether we were subject to Arctic Tern *Sterna paradisaea* attacks. Per nest, we required about 5 min to collect all data.

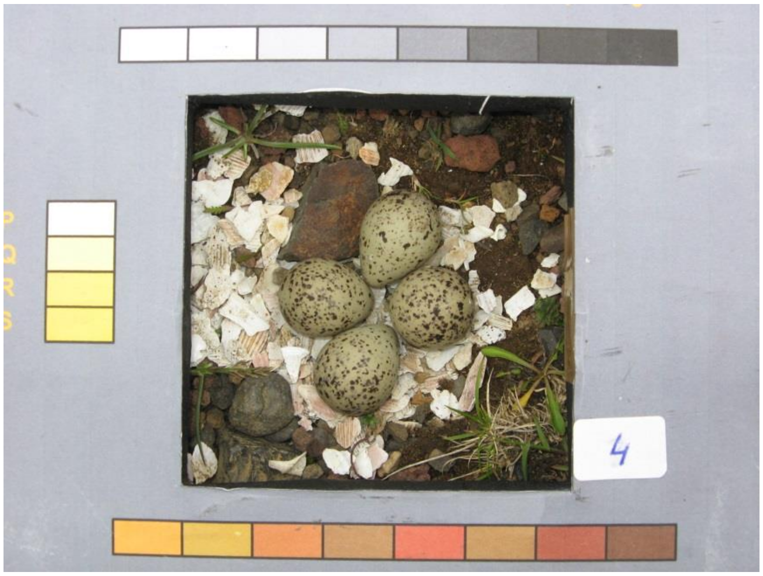

Fig. 1. ‘Standard’ picture of a common ringed plover clutch. The shell fragments at the nest site were most probably collected by the birds themselves.

Properties of clutches, nest sites and nest environments

From the pictures, one of the authors (JvR) scored previously determined characteristics of eggs, clutch, nest site and nest environment. Quite often, it appeared to be very difficult to obtain absolute measures of these characteristics. Therefore, relative measures were used for most characteristics, by comparing all clutches and thus dividing them up into three or four (if possible similarly sized) groups (e.g. small, intermediate, large).

Eggs/clutches – background color was compared with the three color gradients on the wooden frame and scored as the most resembling shade in each of the gradients. Dark and light spots on the egg were distinguished. For each were scored: number, size and distribution; and for the two types of spots together: dispersion over the egg. Homogeneity of the eggs in each clutch was also scored.

Nest sites – within the circle with a radius of 10 cm around the nest were scored: average size of the substrate particles, variation in size of these particles, average color, variation in color, and the presence of stony material, shell fragments, lichens, seaweed, other plant material, and vegetation.

Nest environment – within the circle with a radius of 2 m around the nest: the same characteristics as for the nest site were scored, but the characteristics ‘other plant material’ and ‘vegetation’ were combined. In addition, the presence of attacking arctic terns was scored.

Two-tailed χ^2 tests applying Bonferroni's correction (Zaiontz 2015) were used to examine whether these characteristics varied independently by (1) comparing the different characteristics of the egg (and clutch), (2) those of the nest site, and (3) those of the nest environment, and also by (4) comparing egg (and clutch) characteristics with nest site characteristics, and (5) nest site characteristics with nest environment characteristics. Correlations were determined by Pearson or Spearman coefficients. Significance of the Pearson coefficients was determined by *t*-tests (Zaiontz 2015). Although nests from the same site could potentially be more similar then between sites, we consider this negligible in our study.

Color differences

To enable comparison with studies that focused on background color matching of clutches, we also measured average colors in our images following the method applied by Nguyen et al. (2007) and others. We used the 'nearby' pictures of all nests with at least three eggs (in total 67 nests). For each nest, we determined the average RGB (red, green, blue) scores for three different eggs in a randomly chosen 60×60 pixel sample (equivalent to about 25% of the visible surface of the egg) using GYMP 2.8.14 (Kimball et al. 2014). In addition, average RGB scores in three different 60×60 pixel randomly selected samples from the nest site were determined. As in other studies (Nguyen et al. 2007, Amat et al. 2012, Gómez et al. 2016, Stoddard et al. 2016) RGB scores were converted into L*a*b* scores that allowed to calculate differences between samples (ΔE) (details in Nguyen et al. 2007). We thus obtained for each nest three values of ΔE for egg-egg comparisons, nine values for egg-nest site comparisons, and three values for nest site-nest site comparisons. To avoid influences of lighting condition, differences were only determined for comparisons within the same image. For each image (n=67) we also calculated the average ΔE for the three egg-egg comparisons, for the nine egg-nest site comparisons, and for the three egg-nest site comparisons. To evaluate the effect of light and dark backgrounds, the images were divided into mainly dark volcanic backgrounds (n=29), mixed backgrounds consisting of volcanic substrates with light colored elements such as shell fragments or lichens (n=13), and mainly light colored backgrounds composed of sand or shell fragments (n=25). Paired and unpaired two-tailed *t*-tests (Zaiontz 2015) were used to assess differences between egg-egg, egg-nest site and nest site-nest site comparisons and between dark, mixed and light colored backgrounds.

Clutches in manipulated images

To examine how camouflage is achieved, we manipulated our photos (Fig. 2) using GYMP 2.8.14 (Kimball et al. 2014). First, we produced five images of clutches with their immediate surrounding nest site, clipped out of our 'nearby' pictures. Then, seven additional images of four-egg clutches without any parts of the original surroundings were clipped out (from the five images above plus two extra ones). Each of these 12 images was put down against 17 different backgrounds, yielding 12×17=204 manipulated photos. We used 10 natural backgrounds representing the variation we found (nine from Iceland and one from Terschelling, The

Netherlands). They were cut from our ‘environment’ pictures and included no nest. Besides, four artificial plain backgrounds were used (white, light grey, dark grey and greyish green) and three artificial regularly patterned backgrounds (composed of 800, 300 and 180 identical units). Format (jpeg), width (2048 dots), height (1536 dots) and resolution (X and Y both 314 dots per inch) were the same in all background images.

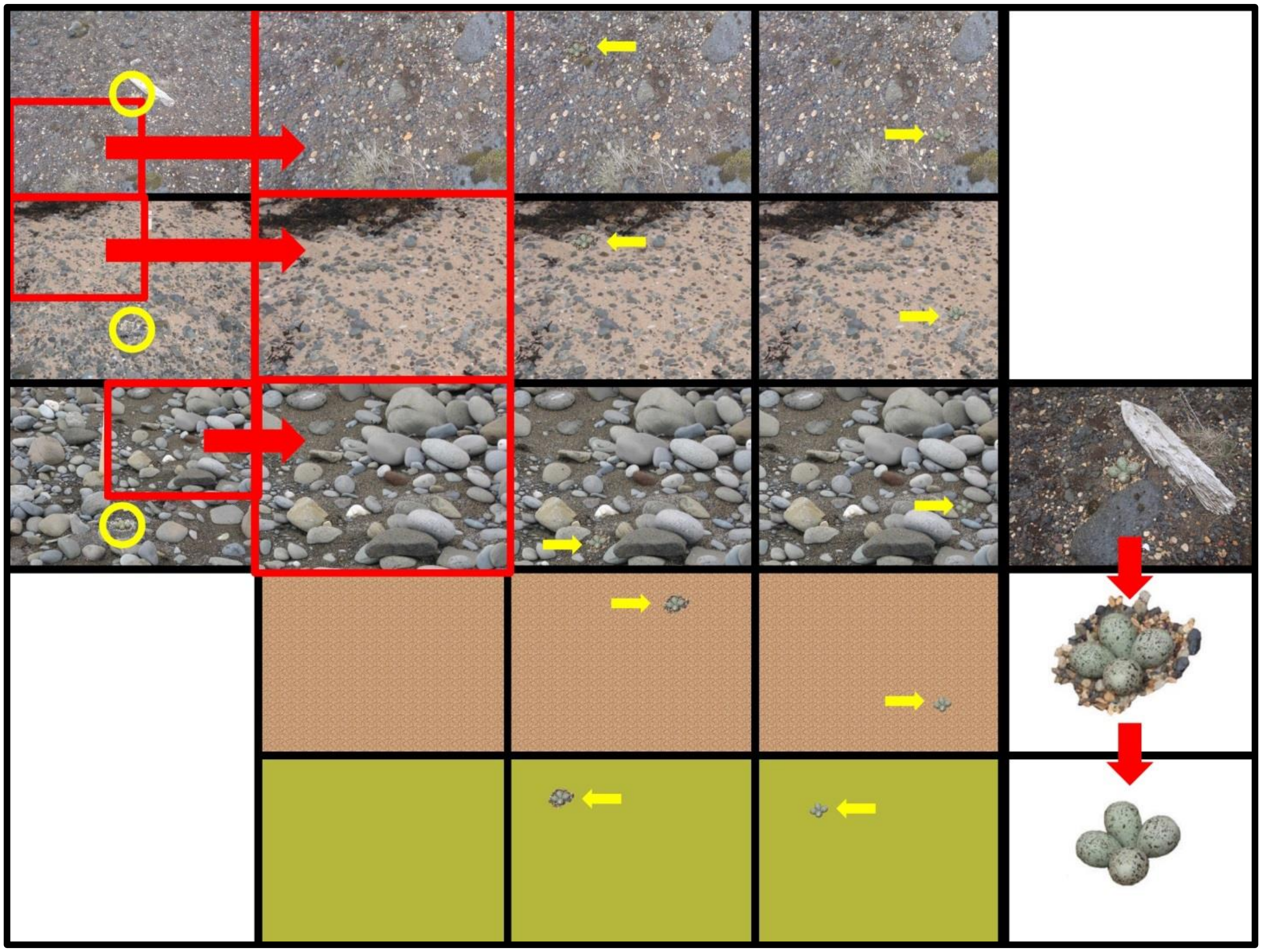

Fig. 2. A few examples of manipulated photos. In the first column, three of the original pictures of the ‘environment’ of a nest are shown. The nest is in the circle. The smaller rectangles within the three pictures were used as experimental backgrounds shown in the second column. In addition, two artificial backgrounds are shown: regularly patterned and plain light green. In the fifth column is shown how nest and clutch were extracted from the ‘nearby’ picture of the nest. That same nest (third column) and clutch (fourth column) was combined with each of the environments in the second column (in this picture the nests and clutches are marked by arrows).

Clutches and nests were put down in the new environments at seemingly suitable sites for nesting, that were evenly scattered over the photo area (upper, lower, left and right part). Our final set of 204 photos was ordered in a quasi-random way with all clutches, nests and backgrounds fairly evenly distributed over the series. This set was displayed to two groups of test persons to determine how quickly the different clutches and nests were found against the different backgrounds. In the first group (persons that were highly experienced in finding meadow bird nests) the 17 test persons had to point to the clutch when it was found to record time (to the nearest 0.1 s) by means of a stopwatch. For the second group (mainly young people interested in technology) the series was reshaped into a game, using GameMaker: Studio, version 1.4.1657 (Overmars et al. 2015). The nine test persons had to click on the eggs to see the next photo. Time (to the nearest 0.01 s) was then automatically recorded and stored in a text file.

For each group of test persons, we composed a 12×17 matrix with the median detection time (median of the scores of all test persons) for each of the 204 photos. Each matrix was then used to make comparisons between the 12 images of nests and clutches and between the 17 environments. This was done by means of paired two-tailed *t*-tests applying Bonferroni-Holm correction (Zaiontz 2015). Each matrix was also used to determine (1) the average detection time for each of the 12 images of nests and clutches (i.e. an average of the scores in 17 environments), and average detection time for each of the 17 environments (i.e. an average of the scores with 12 nests/clutches). Differences between the 17 images of the environment were scored by visual inspection and by means of the GNU Octave software, including the ‘image’ package and the function ‘entropy’ (Eaton et al. 2016). Entropy is a measure of chaos or heterogeneity. The entropy of the elements of an image is computed by this program using a histogram with 256 cells to approximate the distribution of these elements.

RESULTS

Properties of clutches, nest sites and nest environments

Eggs/clutches – variation in background color was small and no association with other clutch characteristics was found. Number, size and distribution of dark and light spots on the eggs, their dispersion over the egg, and homogeneity varied independently: none of the 28 (χ^2) tests was statistically significant.

Nest sites – average size, variation in size and variation in color of substrate particles, and the presence of stony material, shell fragments, lichens, seaweed, other plant material and vegetation did not vary independently: seven of the possible 36 relationships (19%) were statistically significant (χ^2 tests, $P<0.05$).

Nest environment – average size, variation in size and variation in color of substrate particles, and the presence of stony material, shell fragments, lichens, seaweed, vegetation and arctic terns did not vary independently : 11 of the possible 36 relationships (31%) were statistically significant (χ^2 tests, $P<0.05$).

Variation in grey scores of eggs was small, much smaller than of nest sites and nest environments. Grey scores of eggs were not significantly correlated with those of nest sites or nest environments, but grey scores of nest sites were positively correlated with those of nest environments (Table 1). Likewise, other properties of clutches were neither associated with properties of nest sites, nor to those of nest environments. In contrast, properties of nest environments and nest sites were clearly associated (Table 2). In all eight characteristics, scored for both nest sites and nest environments, the two scores were positively correlated (Spearman coefficients, $P<0.01$). Presence of attacking arctic terns was not associated with any of the nest site properties.

Table 1. Correlations between grey scores of eggs, nest sites and nest environments.

Comparison between:	*r*	*t*	df	*P*
Eggs and nest sites	-0.13	-1.18	75	0.24
Eggs and nest environments	-0.02	-0.48	75	0.89
Nest sites and nest environments	0.44	4.25	75	<0.001

Table 2. Associations between the distributions other properties of eggs, nest sites and nest environments (two-tailed χ^2 tests applying Bonferroni's correction, $P<0.01$).

Comparison between:	Number of possible associations	Number significant	%
Eggs and nest sites	72	0	0
Eggs and nest environments	72	0	0
Nest sites and nest environments	81	18	22

Color differences

Our measure for color differences ΔE was relatively small in egg-egg comparisons and considerably larger in egg-nest site and nest site-nest site comparisons (Table 3). In egg-nest site comparisons the average ΔE was significantly smaller in images with mainly light backgrounds compared to mixed backgrounds and dark backgrounds. The average ΔE was not statistically different between mixed and dark backgrounds (Table 4). Remarkably, average ΔE in egg-nest site comparisons was smallest in the two nests from Terschelling (2.80 and 6.23), the only nests that were not from Iceland.

Table 3.

Color differences (ΔE) between eggs and nest sites. Values with a different number of asterisks differ significantly (paired t-tests, one per line, df=65, $P<0.001$).

Comparison between:	mean	SD	*n*
Eggs and Eggs	6.16*	4.17	201
Eggs and nest sites	18.76**	11.21	603
Nest sites and nest environments	16.91**	10.61	201

Table 4.

Color differences (ΔE) between average scores per clutch of eggs and nest site. Values with a different number of asterisks differ significantly (paired t-tests, one per line, df=65, $P<0.05$).

Background:	mean	SD	*n*
Light	14.30*	5.22	25
Mixed	21.07**	7.42	13
Dark	21.58**	8.88	29

Clutches in manipulated images

The two groups – overall average detection time for members of the first group of test persons was 0.95 s and for members of the second group 1.60 s. The difference does not necessarily reflect a difference in skills, as the members of the second group needed extra time to move their pointer to the location of the nest or the clutch.

Nests and clutches – variation among the 12 images in average detection time (average of scores for all 17 backgrounds) where small in each group, but detection time for nests was shorter than for clutches (two-tailed Sign-test, $P<0.05$). For the 10 natural backgrounds, it is shown more clearly in Fig. 3 that in each group average detection time for the five nests was smaller than for the corresponding five clutches (paired *t*-tests; group 1: $t=3.33$, df=8, $P=0.01$; group 2: $t=4.29$, df=8, $P=0.03$).

Backgrounds – variation in average detection time (average of scores for all five nests and seven clutches) was very small among the seven artificial backgrounds. Both against plain and regularly patterned backgrounds, nests and clutches were easily detected. No significant differences (paired *t*-tests) were found in 2×21 comparisons among these backgrounds. In each group, average detection time against the seven artificial backgrounds was in all cases shorter compared to the 10 natural backgrounds (Mann-Whitney *U*-tests, $P<0.001$). Among the 10 natural backgrounds, variation in average detection time (average of scores for all five nests and seven clutches) was considerable (Fig. 3). In 2×45 comparisons among these backgrounds 15 (17%) significant differences were found (paired *t*-tests, $P<0.05$). In each group, nest data (average of the five nests) and corresponding clutch data (average of the five corresponding clutches) were strongly correlated (group 1: $r=0.90$, $t=5.77$, df=8, $P<0.001$; group 2: $r=0.90$, $t=5.93$, df=8, $P<0.001$). Also, the data of the two groups were strongly correlated (nest scores: $r=0.89$, $t=5.44$, df=8, $P<0.001$; clutch scores: $r=0.91$, $t=6.29$, df=8, $P<0.001$) (Fig. 3).

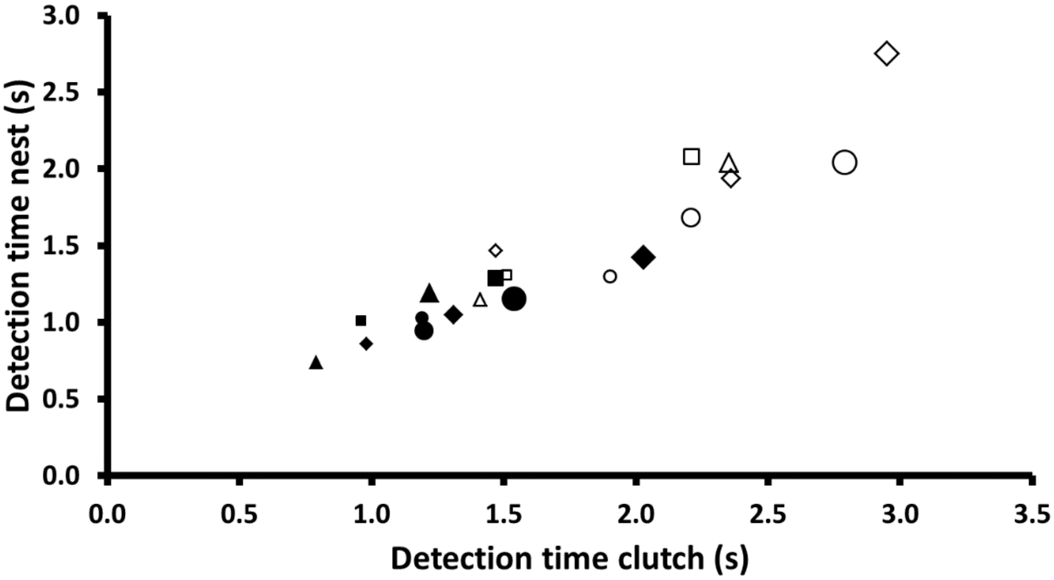

Fig. 3. Relation between average detection time of nests and average detection time of the corresponding clutches for the 10 natural environments. Scores of group 1 are shown as filled symbols and those of group 2 as open symbols. Filled and open symbols that have the same shape and size refer to the same environment.

Nest environment – only one of the characteristics we scored, the average size of the substrate particles, was correlated with the average detection time against the 10 natural backgrounds (group 1: $r=0.71$, $t=2.88$, df=8, $P=0.02$; group 2: $r=0.76$, t=3.33, df=8, P=0.01). As detectability might be influenced by the heterogeneity of the background, we examined the physical properties of the background images. Average detection time (average of scores for all five nests and seven clutches) against the 10 natural backgrounds was positively correlated with the entropy of the image (group 1: $r=0.69$, $t=2.69$, df=8, $P=0.03$; group 2: $r=0.62$, $t=2.22$, $P=0.06$). Remarkably, in each group, average detection time was shortest against the Terschelling background, that also displayed the lowest entropy.

DISCUSSION

The Common Ringed Plover is widespread and breeds successfully in the coastal area of Iceland. Its breeding population is estimated at 50,000 pairs (Gudmundsson 2002, Thorisson et al. 2012). The level of predation on nests is high in this species, both in Iceland (Thorisson 2013) and in other populations (Pienkowski 1984, Liley 1999, Wallander & Adersson 2003), but possibly somewhat higher in populations in temperate areas than in those in the Arctic (Pienkowski 1984). Population size is primarily maintained by the ability to produce quite a number of replacement clutches (Wallander & Adersson 2003, Thorisson 2013). Avian predators use mainly visual cues to detect nests, whereas mammalian predators use other cues in most cases (Pienkowski 1984, Wallander & Adersson 2003). The impact of the different nest predators is unknown, but birds seem to play a major role (Wallander & Adersson 2003). In Iceland, they include various species of gulls, and possibly skuas and Raven *Corvus corax*. In other areas, major avian nest predators besides the gulls are several species of corvids (Wallander & Adersson 2003). It is unlikely that vision of avian nest predators fundamentally differs between Iceland and the other breeding areas of Common Ringed Plovers. Nevertheless, we have no indications that their clutches on dark substrates in Iceland and those on light substrates in other areas experience different risks to be detected by nest predators that highly depend on visual cues.

At most nest sites we studied, the birds seemed to have added various objects: shell fragments, little stones, pieces of lichens, etc. Yet, characteristics of the nest site (including the lining of the nest) were closely associated to those of the nest environments. Variation between clutches, however, was small and could not be associated with variation between nest sites or nest environments. This contrasts, for instance with findings on Japanese Quail *Coturnix japonica*, that produce highly variable clutches and select matching experimental backgrounds for nesting (Lovell et al. 2013). Thus, for Common Ringed Plovers, our first hypothesis (crypsis) could not be supported.

Color differences between clutches and nest sites could be considerable but were relatively small in light colored environments, and smallest (in the same range as the differences between the eggs) for the two nests from Terschelling (The Netherlands). This suggests that crypsis could still be involved in the camouflage of nests on sandy sea shores without volcanic sediments. If so, it would be likely that egg characteristics that contribute to crypsis are subject to natural selection. Then, darker egg types would be more likely to have evolved in the Icelandic population, potentially resulting in geographic variation in egg characteristics, as in many adaptive traits of living organisms (e.g. Jukema et al. 2013, 2015). As we did not find darker egg types in Iceland, camouflage likely relies on other mechanisms than crypsis, at least in that population. The most likely mechanisms are (1) disruptive coloration of the eggs and (2) the choice and adaptation of the nesting habitat by the adults.

We did not investigate the first factor (disruptive coloration), but undoubtedly, disruptive coloration of the eggs of Common Ringed Plovers contributes to their camouflage (e.g. Cuthill et al. 2005, Endler 2006, Schaefer & Stobbe 2006, Stevens et al. 2006, Stevens & Merilaita 2009). Disruptive coloration and patterning are characterized by sharply delimited and conspicuously colored markings, that lead away from the attention of the observer from the virtual outlines of the egg or clutch. In fact the visual system of the observer is tricked (e.g. Stevens & Cuthill 2006, Troscianko et al. 2009). The egg or clutch is not recognized as food and thus ignored. Disruptive coloration and patterning may be supported by characteristics of the environment. Probably the objects (little stones, shell fragments, etc.) that are apparently transported by the adults to the nest, work in this way. Besides, quite a number of nests were settled close to large conspicuous objects, such as stones, pieces of wood or patches of vegetation, that could lead away from the attention of a potential predator.

We tried to study the second factor (choice and adaptation nesting habitat), especially the effect of the environment on camouflage, by examining to what extent human subjects were able to detect clutches and nests in manipulated images. We found that images of Common Ringed Plover clutches (eggs isolated from their original environment) and nests (clutch + nest site) were immediately detected against unstructured (plain colors) or regularly patterned artificial backgrounds. Apparently, such backgrounds are unsuitable for camouflage. Against new natural backgrounds, however, clutches were less easily found. Then clutches were well or fairly well hidden, significantly better than complete nests (Fig 3). Evidently, properties of the nest site make clutches conspicuous against new backgrounds, whereas these properties were assumed to contribute to camouflage in the original environment. We, therefore, conclude that a certain degree of matching between nest site and nest environment is needed to achieve camouflage. This is obviously the case, as, in our set of 77 nests, the scores of the corresponding characteristics of nest sites and nest environments were highly interrelated (Tables 1 and 2).

We also found that the rate at which clutches and nests were detected by human subjects differed between new natural backgrounds (Fig. 3). Heterogeneous backgrounds, typified by a high entropy, served as a better environment for concealing clutches and nests than more homogeneous backgrounds. This is in agreement with many other studies emphasizing the role of heterogeneous backgrounds (e.g. Endler 1978, Merilaita et al. 2001). However, in a study on the Western Snowy Plover *Charadrius alexandrines nivosus* (Colwell et al. 2011), nests on heterogeneous substrates did not survive as good as those on homogeneous substrates, although these heterogeneous substrates were highly preferred for nesting. Remarkably, the Terschelling background, that matched best with the egg colors, was least effective in concealing clutches and nests (T02 in Fig. 3). This was probably caused by its homogeneousness according to its low entropy. Thus, heterogeneous substrates contribute significantly to camouflage, most probably because they support the disruptive patterning of the clutch.

Besides heterogeneity of the background, the scale of dominating structures (e.g. Chiao et al. 2009) may be important for camouflage. Western Snowy Plovers, for instance, prefer environments for nesting with egg-sized stones (Colwell et al. 2011). Survival of their nests is higher in these environments than at sites where such stones are lacking. Namaqua Sandgrouse *Pterocles namaqua* also prefer to nest near stones (Lloyd et al. 2000), but this could not be related to clutch survival. In our study camouflage of clutches (for the human eye) was positively related to the average size of substrate particles, generally stones. These stones could be considerably larger than the eggs, but environments with big stones always contained smaller ones, also egg sized stones. Thus, our finding is not conflicting with the one on Western Snowy Plovers (Colwell et al. 2011).

The extent to which camouflage protects a clutch primarily depends on the perceptual abilities of the predators. We used human subjects for measuring detectability, but humans are – at most – very rare collectors of Common Ringed Plover eggs on Iceland. Probably, the only mammals that present a serious threat to the plover nests are Arctic foxes. These, however, search mainly with the use of smell, whereas we measured visual detection only. The major visual predators of plover eggs are gulls and skuas. The bird's visual system differs from the human system, in particular by its ability to detect smaller wavelengths (UV) by the fourth type of cones in the retina, but for the rest, perception is fairly comparable (e.g. Kevan et al. 2001). Thus, our results provide some level of indication regarding camouflage.

We proposed four hypotheses as to why Common Ringed Plover clutches are well hidden to predators that search visually: (1) eggs and backgrounds match in color and pattern, (2) certain properties of the eggs make them hard to find in almost any environment, (3) camouflage is due to certain properties of the environments chosen and manipulated for nesting by the bird, and (4) camouflage is due to another kind of interaction than close resemblance, between properties of eggs and environments. The first possibility plays a minor role at most. The second possibility, in particular, disruptive coloration and patterning, are suggested as key factors but offer no protection in any environment. We pointed out that the third possibility may also be considered as a key factor. Thus, neither the second, nor the third hypothesis fully explain camouflage of Common Ringed Plover Clutches in Iceland. The fourth hypothesis properly describes the phenomenon, but offers no explanation.

ACKNOWLEDGEMENTS

We thank the following persons: Tómas Grétar Gunnarsson, Vigfús Eyjólfsson and José Alves for sharing their knowledge, for helpful suggestions and for pointing out where we could find the most suitable breeding areas; Jan Jukema, Albert Jukema and Seerp van der Schaar for spotting nests and other help in the field; the specialists in finding meadow bird nests and the visitors and staff of 'De Jonge Onderzoekers Groningen' including a group of students at the 'Willem

Lodewijk Gymnasium Groningen' for completing the test with manipulated images. We also wish to express our gratitude to all the people who contributed to a pleasant stay in Iceland. Finally, we thank José Alves and his team for constructive and helpful comments.

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