FUNCTION OF COLOURED BILL TIPS, STRIPES AND SPOTS IN BREEDING GULLS

PETER N. FERNS & VIOLA H. ROSS-SMITH

School of Biosciences, Cardiff University, Cardiff, CF10 3AX, UK
(fernspn@cardiff.ac.uk)

Received 1 October 2008, accepted 8 April 2009

SUMMARY

FERNS, P.N. & ROSS-SMITH, V.H. Function of coloured bill tips, stripes and spots in breeding gulls. *Marine Ornithology* 37: 85–92.

We used independent contrasts analysis to investigate the function of differently coloured tips, spots and stripes on the beaks of adult gulls. We combined continuous and categorical variables set out in an Open Document Format spreadsheet (available as Appendix 1 at the *Marine Ornithology* web site) that can be adapted for similar analyses in other contexts. Our results show that a uniformly coloured bill occurs in species with a small adult body size and a relatively large egg size (average egg length approximately equal to 14% of body length), whereas a red gonys spot occurs in those with a large body size and a relatively small egg size (average egg length approximately equal to 12% of body length). Both a differently coloured bill tip and a black stripe on the bill occur in species with adult body and egg lengths of intermediate size (average egg length approximately equal to 13% of body length). Egg length also increases more quickly per unit increase in body length in species of intermediate size than in the other groups. Patterned beaks may thus have evolved to focus the pecking response of chicks, which are relatively small at hatching in relation to their parents, red spots being present in cases in which the size difference is greatest. Such adaptations would have enabled adult gulls to evolve larger body sizes, without their eggs and chicks having to increase in size to the same extent.

Key words: Gulls, beak colouration, body size, egg size, comparative analysis, independent contrasts

INTRODUCTION

Some species of gulls have uniformly coloured bills, but many (62% of the species in our sample) have beaks with differently coloured tips, stripes or spots that act as a focus for the pecking of newly hatched chicks as they beg for food (Goethe 1937, Tinbergen & Perdeck 1950, Hailman 1967). In an attempt to understand why, we determined whether adult gulls of those species with newly hatched chicks that are small in relation to the size of the adult are more likely to have such patterned beaks. This work is based on Hailman's (1967) suggestion that gulls with greater bill depths (large species) tend to have only a restricted area of red on the bill (i.e. a red tip or spot), whereas smaller-billed species have uniform bills. We therefore compiled a database of this information for as many species of gulls as possible in order to address the issue using modern comparative statistical methods. We suggest that the most plausible reason for any size-related difference is that concentrating a small chick's pecking on a particular part of the bill is more effective than is unfocussed pecking in stimulating the adult to regurgitate food. As well as encouraging the chick to peck, the tip of the bill or the gonys (where stripes and spots are located), might be more sensitive than are other parts of the beak to the feeble pecking of a small chick, or a small chick might more effectively occupy the parent's visual field when pecking there.

The importance of taking phylogenetic effects into account during comparative studies of this sort is now well established (see Carvalho *et al.* 2006 for a critical review). A difficulty occurs when studying a group of species that share biologic traits inherited from a common ancestor, because the existence of such characters cannot be treated as if they were independent evolutionary events in each species. Such independence is, of course, an essential prerequisite of most statistical tests, and ignoring phylogeny can therefore result in pseudoreplication and, hence, incorrect conclusions.

One of the most widely used methods of eliminating phylogenetic pseudoreplication is to analyse evolutionarily independent contrasts (differences between sister taxa) rather than the raw species values themselves (Felsenstein 1985, Harvey & Pagel 1992). Several freeware packages facilitate such analyses—for example, CAIC (Purvis & Rambaut 1995), PDTREE (Garland & Ives 2000), COMPARE (Martins 2004), APE (Paradis *et al.* 2004). Freeware packages are also available for generalised least-squares and maximum-likelihood models, which offer additional advantages over the independent contrasts approach, including greater refinement of the evolutionary model adopted (Grafen 1989, Blomberg *et al.* 2003, Freckleton *et al.* 2002, McKechnie *et al.* 2006). Lists of relevant software packages and their capabilities are available on J. Felsenstein's web pages (http://evolution.genetics.washington.edu/phylip/software.html).

Many of these software packages are command line programs, which cannot always combine continuous and categorical variables in the same analysis, a factor that may discourage field workers from carrying out comparative analyses that take phylogeny into account. We therefore set out our calculations in an Open Document Format spreadsheet (available as Appendix 1 at the *Marine Ornithology* web site), which we hope will encourage more people to test their ideas using a phylogenetically valid approach. Modifying such a spreadsheet is easier than starting from scratch and leaves the investigator in full control of the analyses, able to fine-tune sets of calculations to suit the hypotheses being tested. The spreadsheet can also be manipulated to extract the maximum information from a mixture of continuous and categorical variables. Full instructions on how to use and modify the spreadsheet are also provided (Appendix 2).

METHODS

Our database included information on two continuous variables: adult gull body length (or length range midpoint) of both sexes combined, and egg length. We used these variables because they were the largest widely available linear measurements reflecting adult body size (male and female combined) and chick size. Very few measurements of chick size at hatching are available in gulls, and egg length is a reasonably good proxy for egg size, and therefore for newly-hatched chick size, in other species (Göth & Evans 2004, Abanikannda & Leigh 2007). The database also included four categorical variables based on the colour and pattern of the adult bill during the breeding season (Fig. 1). These were the presence or absence of a differently coloured bill tip, a black stripe or a red spot and a score derived from the three (0 = uniform colour; 1 = differently coloured bill tip or a black stripe, or both; 2 = red spot).

We compiled information for 45 species, based on the taxonomy in Pons *et al.* (2005), using the Integrated Taxonomic Information System (http://www.itis.gov/) for English and scientific names, except where recent studies indicate the existence of new species [i.e. Caspian Gull *Larus cachinnans,* Yellow-legged Gull *L. michahellis* and North American Herring Gull *L. smithsonianus* (Liebers *et al.* 2001, Crochet *et al.* 2002, Collinson *et al.* 2008)]. The sources of the morphometric data are shown in Fig. 1. Both continuous variables passed a normality test after square root transformation (body length, Kolmogorov–Smirnov $d_{\max} = 0.107$, $P > 0.150$; egg length, $d_{\max} = 0.125$, $P = 0.077$), which was therefore used.

Molecular phylogenetic information is available for most species of gulls (Pons *et al.* 2005) based on mitochondrial DNA (deposited at Genbank http://ww.ncbi.nlm.nih.gov/Genbank/index.html), and branch lengths for the phylogeny (in Newick format) were obtained directly from the first of these authors. We looked for associations between the values of all these variables and their phylogenetic history using the freeware package Phylogenetic Independence 2.0 (Reeve & Abouheif 2003) which employs *C*-statistics to test continuous variables and runs tests for discrete ones. The spreadsheet we used to calculate independent contrasts is in OpenOffice (.ods) format (Appendix 1), available at the *Marine Ornithology* website with instructions (Appendix 2).

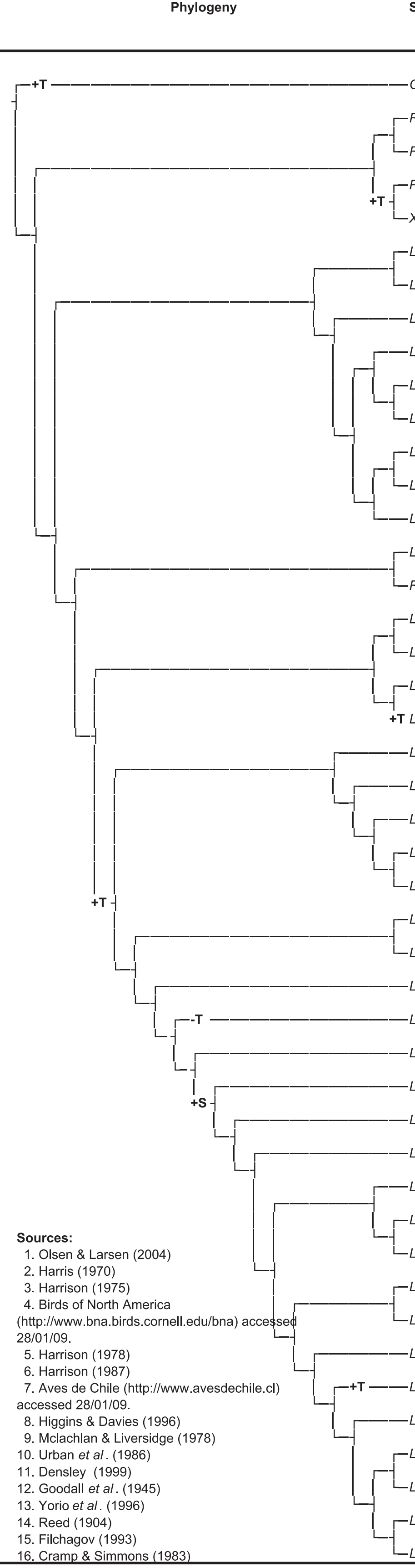
First, we omitted species for which we were unable to obtain egg lengths, adjusting the phylogeny (including branch lengths) accordingly. Then, we calculated contrasts by Felsenstein's (1985) method. In addition, we included Harvey & Pagel's method (1992) in the spreadsheet, assigning equal length to all branches, to see if our conclusions were sensitive to the method of analysis employed. Transitions in the categorical variables were allocated on the basis of out-group information (i.e. their state in the most closely related group of birds, the terns) and parsimony (i.e. the smallest number of changes of state in the tree necessary to achieve the observed state in each species; see Fig. 1). The basal nodes of the tern phylogeny have a uniform bill (Bridge *et al.* 2005), and a uniform bill was therefore assumed to be the ancestral condition in gulls. The independent contrasts for body length (the explanatory variable) were constrained to be positive, as recommended by Garland *et al.* (1992), though this constraint is not essential.

The phylogeny shows that gulls with a red spot on the lower mandible fall into a completely separate lineage within the Laridae (Fig. 1). This condition also holds true if all the species examined by Pons *et al.* (2005) are included, not just those with available egg measurements. Therefore, the first hypothesis we tested was whether species with a red spot on the bill had relatively smaller eggs than the others. To extract the information needed for this test, the spreadsheet (Appendix 1) needs to be separated into two groups by breaking the tree at the point of transition, calculating independent contrasts within each group, and then comparing the groups. The tree has to be broken to prevent any effects the red bill spot may have on the continuous variables from diffusing back up the tree to the species that lack it. This procedure is identical to that used by Garland & Janis (1993) and recommended by Purvis & Rambaut (1995), except that the division into two groups is not at the basal node. It is also similar to the method for testing grade effects in CAIC (Purvis & Rambaut 1995). To achieve this break, we divided the worksheet into upper and lower halves by deleting the node joining the last member of the clade without a red spot (Ring-billed Gull *L. delawarensis*) and the clade with a red spot (starting with the Western Gull *L. occidentalis*). We then calculated the contrasts separately (only the formulae for the single node joining *L. delawarensis* to *L. canus* needs to be altered to achieve this separation).

The foregoing method generates one less contrast than are present in the complete tree, because the tree has been broken at one of the nodes. Essentially, the within-category contrasts contain the information in the slopes of the ordinary species regression lines in Fig. 2, corrected for phylogeny. However, a contrast between the two groups at the point of evolutionary transition can also be calculated (it is actually the difference between the parental node of the group with a red spot on the bill and its sister in the other group, the Ring-billed Gull). This contrast contains information about whether the intercepts of the regression lines are different (providing the slopes are not different), corrected for phylogeny.

Examination of the phylogeny suggests that the ancestral gull had a uniformly coloured bill, but as body size increased, the upper and lower mandibles of the bill developed either a differently coloured tip or a black stripe. Only when body size increased even further did they instead evolve a red spot on the lower mandible. Our second hypothesis was therefore whether this series of transitions was also linked to changes in relative egg size. We combined species with a differently coloured tip and a black stripe because the phylogeny indicates that the latter probably evolved only three times, and on two of those occasions it co-evolved with a differently coloured tip.

The contrasts were divided into three groups on the basis of the categorical bill variables (uniform; coloured tip or black stripe; red spot). To achieve this division, calculation of the values for the continuous variables at higher nodes were made after breaking the tree at each transition and isolating the species or group of species. The logic is that when a new category evolves (such as when a gull species evolves a red spot), the relationship between the continuous variables makes a step change. It would be wrong to allow the



Species	Branch length (×10³)	Body length (cm)	Source	Egg length (mm)	Source	Tip	Black stripe	Red spot	Bill score
Creagrus furcatus	136.3	57.5	1	66.1	2	1	0	0	1
	400.8								
Rissa tridactyla	48.0	39.0	1	55.9	3	0	0	0	0
	55.4								
R. brevirostris	93.8	37.5	1	58.0	4	0	0	0	0
	26.5								
Pagophila eburnea	78.7	41.5	1	60.7	3	1	0	0	1
	73.2								
Xema sabini	83.2	31.0	1	44.4	3	1	0	0	1
	56.3								
Larus genei	38.8	42.0	1	55.7	3	0	0	0	0
	37.6								
L. philadelphia	97.0	29.0	1	49.0	5	0	0	0	0
	106.0								
L. maculipennis	16.4	37.0	6	52.0	7	0	0	0	0
	39.4								
L. bulleri	6.7	36.0	6	50.1	8	0	0	0	0
	11.6								
L. scopulinus	10.8	38.8	8	53.1	8	0	0	0	0
	6.4								
L. novaehollandiae	13.4	40.5	8	52.8	8	0	0	0	0
	13.7								
L. cirrocephalus	6.6	40.5	1	53.9	9	0	0	0	0
	9.7								
L. hartlaubii	6.4	38.0	9	52.3	10	0	0	0	0
	6.9								
L. ridibundus	16.6	36.5	1	51.9	3	0	0	0	0
	18.5								
L. minutus	164.8	26.0	1	41.5	3	0	0	0	0
	57.6								
Rhodostethia rosea	56.0	30.0	1	43.6	11	0	0	0	0
	52.8								
L. modestus	41.9	45.0	1	58.3	12	0	0	0	0
	28.9								
L. scoresbii	53.7	44.0	6	60.9	13	0	0	0	0
	38.5								
L. atricilla	14.5	38.5	1	54.0	5	0	0	0	0
	9.3								
L. pipixcan	21.3	35.0	1	52.0	5	1	1	0	1
	34.4								
L. melanocephalus	31.1	38.0	1	53.7	3	1	1	0	1
	14.8								
L. audouinii	37.3	50.0	1	62.2	3	1	1	0	1
	14.8								
L. leucophthalmus	33.4	44.0	1	56.0	3	1	0	0	1
	22.6								
L. ichthyaetus	88.3	59.0	1	77.9	3	1	1	0	1
	7.3								
L. hemprichii	18.0	43.5	1	57.8	10	1	1	0	1
	36.2								
L. pacificus	23.6	62.0	6	75.4	8	1	0	0	1
	7.7								
L. belcheri	46.5	50.0	1	64.0	7	1	1	0	1
	18.7								
L. heermanni	41.4	47.5	1	62.2	14	1	0	0	1
	12.7								
L. canus	15.7	42.5	1	57.6	3	0	0	0	0
	19.6								
L. delawarensis	9.1	45.0	1	59.0	5	0	1	0	1
	17.5								
L. occidentalis	4.2	64.0	1	72.0	5	0	0	1	2
	12.2								
L. livens	6.4	63.5	1	73.2	4	0	0	1	2
	5.6								
L. dominicanus	7.5	59.5	1	70.4	8	0	0	1	2
	16.4								
L. armenicus	12.9	56.0	1	68.1	15	0	0	1	2
	8.6								
L. marinus	3.1	69.5	1	77.0	5	0	0	1	2
	3.3								
L. michahellis	6.2	55.0	1	69.0	16	0	0	1	2
	6.0								
L. cachinnans	2.9	62.0	1	71.8	15	0	0	1	2
	3.3								
L. argentatus	9.6	61.0	1	69.8	3	0	0	1	2
	4.2								
L. fuscus	9.0	53.0	1	67.6	3	0	0	1	2
	3.3								
L. californicus	8.9	48.0	1	68.0	5	0	1	1	2
	9.0								
L. smithsonianus	2.9	59.0	1	70.0	5	0	0	1	2
	3.5								
L. glaucescens	9.2	63.0	1	73.0	5	0	0	1	2
	6.2								
L. hyperboreus	3.3	66.0	1	76.8	3	0	0	1	2
	5.9								
L. thayeri	5.9	60.5	1	74.0	5	0	0	1	2
	3.2								
L. glaucoides	8.8	56.0	1	69.0	5	0	0	1	2

Sources:
1. Olsen & Larsen (2004)
2. Harris (1970)
3. Harrison (1975)
4. Birds of North America (http://www.bna.birds.cornell.edu/bna) accessed 28/01/09.
5. Harrison (1978)
6. Harrison (1987)
7. Aves de Chile (http://www.avesdechile.cl) accessed 28/01/09.
8. Higgins & Davies (1996)
9. Mclachlan & Liversidge (1978)
10. Urban *et al*. (1986)
11. Densley (1999)
12. Goodall *et al*. (1945)
13. Yorio *et al*. (1996)
14. Reed (1904)
15. Filchagov (1993)
16. Cramp & Simmons (1983)

Fig. 1. Spreadsheet showing the data used in the tests (sequence based on Pons *et al.* 2005). Letters in the phylogeny indicate the most parsimonious placement of the following evolutionary events: +T = evolution of a differently coloured tip or a black stripe; –T = loss of T; +S = replacement of T with a red spot.

influence of, for example, increased body size as a consequence of the red spot, to diffuse back up the tree to those nodes that lack it (as would happen with a normal contrasts analysis). If a species reverts to an earlier condition (and, in this case, loses the red spot), then it too must be isolated.

Contrasts at points of evolutionary transition between categorical variables can also be calculated, but they need to be treated differently from the within-group contrasts. They should not be constrained to be positive like the within-group contrasts, but rather they should be corrected so as to be positive if associated with changes in one direction in a continuous variable or negative if associated with changes in the opposite direction. Contrasts involving the gain of a character should be the opposite in sign (for a change in a particular direction in a continuous variable) from those involving the loss of a character. The null hypothesis in any test of either losses or gains is that they have an expected mean contrast value of zero (Purvis & Rambaut 1995).

The process is illustrated in Fig. 3. The transitions are first allocated on the basis of parsimony. The contrasts associated with evolutionary transitions in the categorical variables are then extracted, starting with those at the tips of the tree. The next step is to proceed back up the tree, extracting higher node transitions and breaking the tree. When all the transitions have been removed, only the hierarchically-contained contrasts within the various isolated sets of character states remain, and these too can be extracted. The number of degrees of freedom associated with the extracted contrasts should be reduced by one for each tip or node they share with a between-group contrast [e.g. Y_1 in Fig. 3(a) and Y_2 in Fig. 3(b)], because these are fixed and not free to vary. The contrasts should be carefully labelled according to the transition that they represent or the character state they lie within. All the contrasts within a group should be made positive for the independent variable; the signs of contrasts involving transitions should be adjusted if necessary.

RESULTS

Species-level analysis

We observed no significant difference in either body length or egg length between the species with a differently coloured bill tip, a black stripe, or both, when those species were treated as though they were independent entities (ANOVAs: body length—$F_{2,11} = 0.62$, $P > 0.200$; egg length—$F_{1,11} = 1.29$, $P > 0.200$), and so we combined those categories. The distribution of body lengths showed signs of bimodality [Fig. 4(a)], with most of the species in the larger mode (approximately 80%) having a red spot. Examination of the phylogeny (Fig. 1) showed a relatively recent radiation of these larger species in which egg size has not increased proportionally as fast as body size. The difference was apparent when egg size was expressed as a percentage of body length [Fig. 4(b)] and is reflected in the percentage coefficient of variation of egg size in this group: at 2.2, it was much less than the 4.6 variation in body size. In species with a uniform bill, the relative difference between the coefficients of variation in egg size (4.8) and body size (6.8) was not as great (29% rather than 52%). The egg length of species with a uniform bill constituted 14.2% ± 1.1% of adult body length (mean ± standard deviation, n = 17), but that of species with a red spot was only 12.0% ± 0.8% (n = 15). The egg length of species with differently coloured bill tip, or a black stripe, was intermediate (13.3% ± 1.0%, n = 13). Although small, these differences are highly significant if species are treated as independent entities (ANOVA: $F_{2,42} = 20.80$, $P < 0.0005$). Tukey tests showed that this significance was a consequence of species with a red spot being significantly different from both of the other two groups; the latter were not significantly different from one another.

Another analysis that treats species as though they were independent showed that the slope of the regression line relating egg length to adult body length is shallower (and is located in the upper part of the body size range) in species with a red spot on the lower mandible than it is in species with other bill patterns [Fig. 2; egg length analysed by ANCOVA: body length effect—$F_{1,41} = 113.70$, $P < 0.0005$; spot effect—$F_{1,41} = 9.08$, $P = 0.004$; body length versus spot interaction—$F_{1,41} = 9.21$, $P = 0.004$; slope of species without a spot ± 95% confidence interval (CI)—0.778 ± 0.095, $R^2 = 0.909$; slope of those with a spot ± 95% CI—0.434 ± 0.145, $R^2 = 0.763$]. A similar ANCOVA using bill score rather than the presence of a red spot as a factor showed a similar result (body length effect: $F_{1,39} = 175.15$, $P < 0.0005$; bill score effect: $F_{2,39} = 4.48$, $P = 0.018$; body length versus bill score interaction: $F_{2,39} = 4.55$, $P = 0.017$), but a comparison that included only species with a uniform bill and those with a black stripe or differently coloured tip, showed

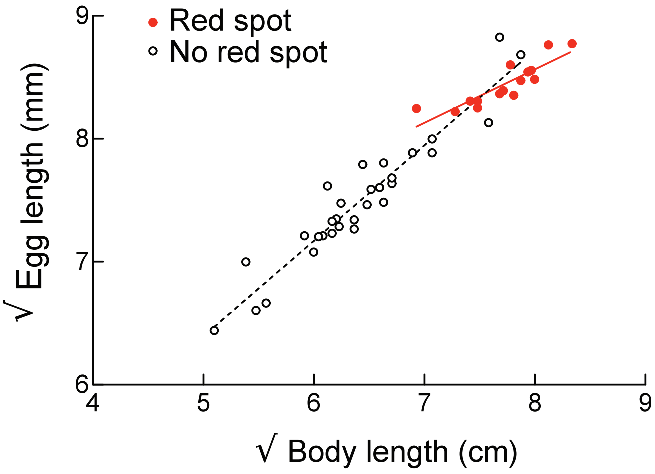


Fig. 2. Regressions of egg length against body length for gull species with (red circles, red line) and without (black open circles and dashed line) a red spot on the lower mandible.

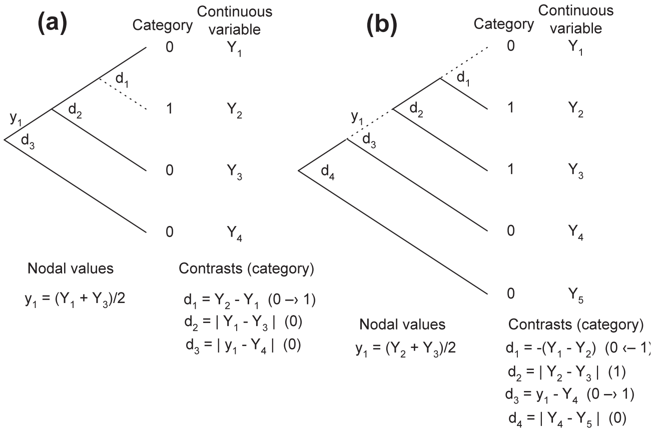


Fig. 3. Hypothetical cladogram illustrating how contrasts can be calculated when breaking the tree (a) at a single evolutionary event involving a transition at a tip (0 → 1), and (b) at two points: a single transition at a higher node (0 → 1) and a reversal at a tip (0 ← 1).

no significant difference in slope or elevation (body length: $F_{1,26} = 171.62$, $P < 0.0005$; bill score: $F_{1,26} = 0.44$, $P > 0.200$; interaction: $F_{1,26} = 0.44$, $P > 0.200$).

Using Reeve & Abouheif's test (2003), the continuous variables were both significantly phylogenetically constrained (body length C-statistic: 0.659, $P < 0.001$; egg length C-statistic: 0.634, $P < 0.001$). Therefore, to avoid taxonomic pseudoreplication, species should not be treated as independent, and some form of comparative analysis that takes account of phylogeny must be undertaken if the above conclusions are to be substantiated.

Independent contrasts analysis

Unlike the original species values, the independent contrasts were not phylogenetically constrained (body length C-statistic: 0.094, $P > 0.200$; length C-statistic: 0.076, $P > 0.200$), and can thus be treated as evolutionarily and statistically independent. To determine whether the standardised contrasts required any further adjustment, we regressed them against their standard deviations as recommended by Garland *et al.* (1992). In no case was a statistically significant relationship observed ($P > 0.050$).

Dividing the phylogeny into two groups on the basis of the red bill spot, we observed a significant difference between the slopes of the regression lines of the two sets of contrasts ($F_{1,39} = 7.28$, $P = 0.010$). We can thus confirm that the relationship between egg length and body length differs significantly in slope in species of gulls with and without a red spot on the lower mandible, and that the slope is shallower in the former (slope ± 95% CI with red spot: 0.504 ± 0.132, $R^2 = 0.776$; without red spot: 0.753 ± 0.117, $R^2 = 0.861$). To test whether the evolution of a differently coloured bill tip or a black stripe occurred in intermediately-sized gulls, we allocated the transitions on the basis of parsimony (Fig. 1). Seven transitions were needed to do so: five gains of a coloured tip or black stripe and one loss, plus one gain of the red spot. One of the gains of a black stripe occurred in a species with a red spot, the California Gull (*L. californicus*). Reeve & Abouheif's (2003) runs test revealed that these categorical changes were phylogenetically constrained ($P < 0.001$). If there had been any doubt about the locations of transitions based on out-groups and parsimony, we could have tested all the alternatives.

Initial examination of the transitions between various bill categories showed that the body length contrasts involving the addition or loss of a differently coloured tip or black stripe to or from a uniform bill were not significantly greater than zero (one-tailed $t_4 = 1.55$, $P = 0.091$), nor were the egg length contrasts (one-tailed $t_4 = 0.91$, $P = 0.202$). Next, the slopes of the regression lines for the three within-category sets of contrasts were compared. A significant difference between them was observed (ANCOVA: $F_{2,30} = 6.96$, $P = 0.003$), with those with a differently coloured tip or black stripe being much steeper (mean slope ± 95% CI: 0.928 ± 0.197, $R^2 = 0.946$) than those with a red spot (0.547 ± 0.122, $R^2 = 0.898$); slopes with a uniform bill were very slightly shallower still (0.545 ± 0.180, $R^2 = 0.766$). This finding remained the case even when an outlier (the contrast involving the largest species—the Great Black-backed Gull *L. marinus*) was removed (Fig. 5; $F_{2,29} = 5.48$, $P = 0.010$; slope of red spot group: 0.604 ± 0.198, $R^2 = 0.821$). The slopes of the regressions for uniform bills and bills with a red spot did not differ significantly from one another (outlier removed, two-tailed $t_{23} = 0.48$, $P > 0.200$), but those for the red spot and tip or black stripe groups did (outlier removed, two-tailed $t_{17} = 2.57$, $0.020 > P > 0.010$).

None of these findings was significantly changed using contrasts calculated by Harvey & Pagel's method (1992), which has the advantage that it can be used when information on branch lengths is not available. If bill score is treated as though it were a continuous variable, and its effects allowed to diffuse back up the tree, its effect is not significant (multiple regression of egg length contrasts on bill score contrasts: $t_{42} = 0.86$, $P = 0.393$; on body length contrasts: $t_{42} = 9.49$, $P < 0.0005$). These results suggest that dealing with discrete variables by breaking the tree, as we have done, provides greater statistical power than does treating them as though they were continuous, even though it is a more complicated procedure.

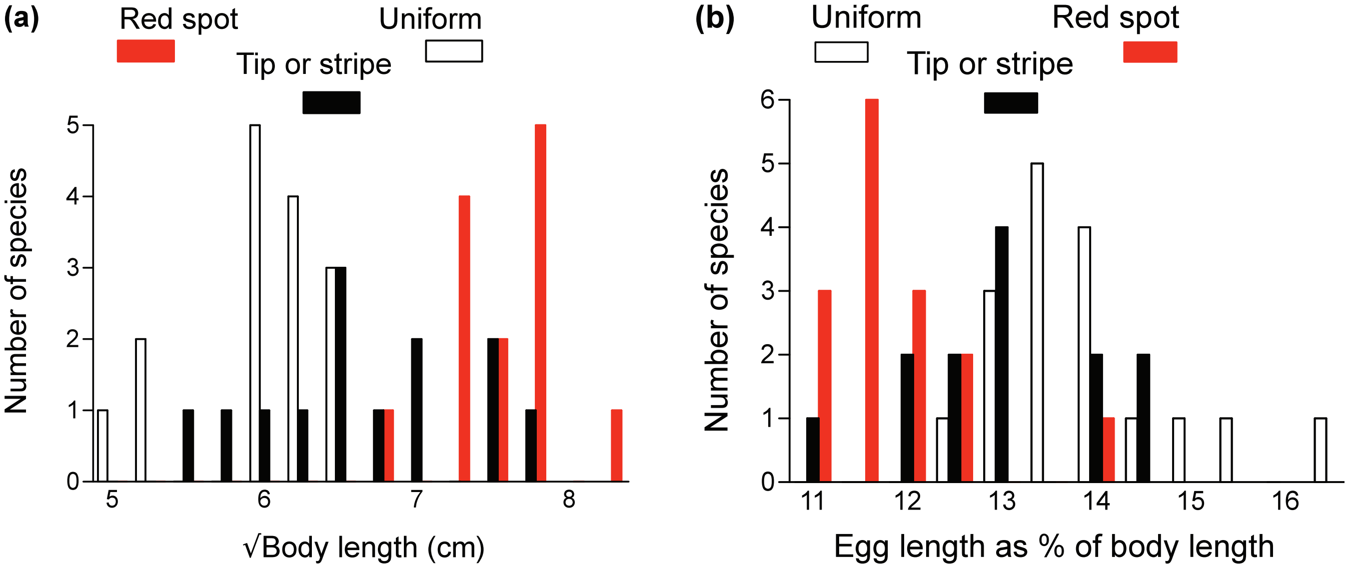


Fig. 4. Distribution of (a) body length and (b) egg length expressed as a percentage of body length, in gulls with different bill types. Tip or stripe = differently coloured tip or black stripe.

DISCUSSION

Compared with other marine birds, small gulls lay reasonably large eggs, whereas large gulls lay eggs of intermediate size (Lack 1968). Our results show that relative egg size also varies with beak colour. Small gulls tend to have a uniformly coloured bill. The presence of a differently coloured bill tip, or a black stripe, occurs in larger species of gulls in which egg size increases almost as steeply (in relative terms) as body size. A red spot is present in gulls with the largest adult body sizes, but in which egg size increases relatively less steeply with increased body size. This finding is consistent with the idea that the pecking of small chicks needs to be directed to a particular part of the adult's bill for some reason. Based on our calculations, focussing of the chicks' pecking seems to be needed in gull species in which egg length falls below about 13% of adult body length. Many other seabirds lay eggs that are relatively smaller than this, but they feed their rather feeble newly-hatched young directly from the bill without any solicitation by begging (e.g. many of the Pelecaniformes).

This situation raises two questions. First, what is the advantage of large body size in gulls, given that a group of large species with a red spot on the bill has evolved relatively recently? Second, why do larger gulls lay relatively small eggs? Götmark (1984) has already suggested an answer to the first question: Namely, that larger, more powerful species can both exploit larger prey and dominate smaller species in competition for smaller prey. A possible answer to the second question lies in the fact that the modal clutch size of three in most gulls is relatively large for a seabird, reflecting the fact that many species are inshore, shoreline and terrestrial foragers with quite flexible nest site requirements (cliffs, cliff tops, roof tops, offshore islands, islets, peninsulas, sand dunes, open ground). These two features of their ecology mean that most species can deliver food quite quickly to the growing brood (Lack 1968). Species that are not able to do so, such as the offshore feeders, tend to have smaller clutches—for example, the Swallow-tailed Gull *Creagrus furcatus* and Black-legged Kittiwake *Rissa tridactyla* (modal clutch sizes of one and two eggs respectively).

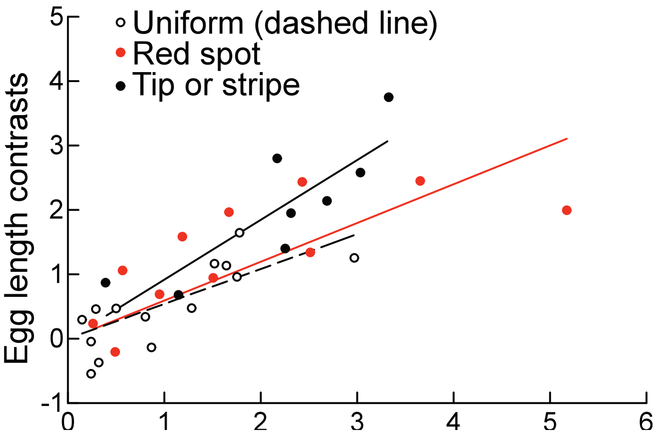


Fig. 5. Regressions of egg length contrasts against body length contrasts in three groups of gulls: those with a uniformly coloured bill (black open circles, dashed line), those with a red spot on the lower mandible (red circles and line, outlier omitted), and those with a differently coloured tip or a black stripe (black closed circles and continuous line).

The use of readily available, but relatively insecure nesting sites means that gull eggs and young are vulnerable to predation, and gulls thus have a very short incubation period (Lack 1968). One possible explanation of the relatively smaller eggs in larger species is thus that it helps keep the incubation period short. This hypothesis seems to be contradicted by the fact that supplementary feeding during egg formation increases egg size in some species such as the Lesser Black-backed Gull *L. fuscus* (Bolton *et al.* 1992). More consistent with the latter finding is the possibility that the larger gull species lay relatively small eggs because they have difficulty finding sufficient food resources to form three eggs within the normal gull egg-laying period. This interpretation is supported by the fact that gulls, terns, skuas and skimmers are the only seabirds in which courtship feeding occurs, and such feeding may be essential for rapid egg formation. Female gulls usually beg in the same manner as large chicks do—that is, by hunching the body and head tossing (e.g. Velando 2004). They also peck at the beak, especially the red sides of the gape (Brown 1967).

Differently coloured adult bill tips, stripes or spots may simply be necessary to stimulate relatively small gull chicks to beg. Alternatively, their begging pecks may need to be focussed on a particular part of the adult bill to stimulate parental food regurgitation in the larger species, or localised pecking may help to initiate a dietary switch in adults so that they bring smaller food items that are easier for young chicks to swallow and digest. Because of the difficulty that newly hatched chicks among the larger species of gulls have in swallowing large items, or because of their different nutritional needs, many of those gulls switch foods when feeding those chicks—for example, the Ring-billed, Western, Herring and Audouin's Gulls *L. audouinii* (Kirkham & Morris 1979, Annett & Pierotti 1989, Bukacińska *et al.* 1996, Pedrocchi *et al.* 1996). As well as engaging and focussing the attention of small chicks, a coloured bill tip, stripe or spot might also stimulate begging that is sufficiently different from that of females or large chicks (i.e. pecking at the tip or the gonys, rather than the head tossing and pecking at the gape) that it signals the need for their parents to initiate this dietary switch.

The fact that egg size increases less quickly than body size is true of most groups of birds and of birds as a whole (Ricklefs 1974, Blueweiss *et al.* 1978). What is especially critical in gulls, however, is that as soon as possible after hatching, their young should develop quickly so that they can temporarily leave the nest and hide when threatened by predators. Differently coloured bill tips, stripes and spots contribute to this behaviour by ensuring prompt and efficient food delivery to the chicks. Such features may therefore be subject to sexual as well as natural selection, because choosing mates without them is likely to lead to reduced reproductive output. The colour of the red spot has been shown to be subject to such selection in Yellow-legged Gulls (evidence cited by Pérez *et al.* 2008).

The advantage of using a spreadsheet rather than a freeware package to carry out our comparative analyses was that it allowed us to identify and analyse trends in our data (e.g. within-clade patterns) that might have been overlooked had we used a standard software package. It also helped us formulate new ideas to test in future, such as the suggestions raised earlier here. It so happens that many of these trends and suggestions would be quite hard to test using existing packages. Testing of a range of plausible placements for character transitions, if there is any doubt as to their location, also becomes a possibility. In this case, we were able to allocate patterning on the basis of out-group information, which is another feature that can be difficult to achieve with a package. Terns provide the most relevant out-group in this case (Pons *et al.* 2005), and 76% of tern species lack a multicoloured bill (Bridge *et al.* 2005). Finally, compiling such a spreadsheet is an efficient and effective way for new users to find out how independent contrasts methods work.

ACKNOWLEDGEMENTS

We thank Jean-Marc Pons for making the branch lengths of his gull phylogeny available and Rob Thomas for commenting on a draft of the paper. Falk Huettmann and Hanno Sandvik made numerous improvements to the manuscript. One of us (VHRS) was funded by a Cardiff University Research Studentship.

REFERENCES

ABANIKANNDA, O.T.F. & LEIGH, A.O. 2007. Allometric relationships between composition and size of chicken table eggs. *International Journal of Poultry Science* 6: 211–217.

ANNETT, C. & PIEROTTI, R. 1989. Chick hatching as a trigger for dietary switching in the Western Gull. *Colonial Waterbirds* 12: 4–11.

AVES DE CHILE (http://www.avesdechile.cl) accessed 28/01/09.

BIRDS OF NORTH AMERICA (http://www.bna.birds.cornell.edu/bna) accessed 28/01/09.

BLOMBERG, S.P., GARLAND, T. & IVES, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717–745.

BLUEWEISS, L., FOX, H., KUDZMA, D., NAKASHIMA, D., PETERS, R. & SAMS, S. 1978. Relationships between body size and some life history parameters. *Oecologia* 37: 257–272.

BOLTON, M., HOUSTON, D. & MONAGHAN, P. 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *Journal of Animal Ecology* 61: 521–532.

BRIDGE, E.S., JONES, A.W. & BAKER, A.J. 2005. A phylogenetic framework for the terns (Sternini) inferred from mtDNA sequences: implications for taxonomy and plumage evolution. *Molecular Phylogenetics and Evolution* 35: 459–469.

BROWN, R.G.B. 1967. Courtship behaviour in the Lesser Black-backed Gull, *Larus fuscus. Behaviour* 29: 122–153.

BUKACIŃSKA, M., BUKACIŃSKI, D. & SPAANS, A.L. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). *Auk* 113: 300–309.

CARVALHO, P., DINIZ-FILHO, J.A.F. & BINI, L.M. 2006. Factors influencing changes in trait correlations across species after using phylogenetic independent contrasts. *Evolutionary Ecology* 20: 591–602.

COLLINSON, J.M., PARKIN, D.T., KNOX, A.G., SANGSTER, G. & SVENSSON, L. 2008. Species boundaries in the Herring and Lesser Black-backed Gull complex. *British Birds* 101: 340–363.

CRAMP, S. & SIMMONS, K.E.L. (Eds). 1983. The birds of the Western Paleartic. Vol. III. Oxford: Oxford University Press. 913 pp.

CROCHET, P.A., LEBRETON, J.D. & BONHOMME, F. 2002. Systematics of large white-headed gulls: patterns of mitochondrial DNA variation in western European taxa. *Auk* 119: 603–620.

DENSLEY, M. 1999. *In search of Ross's Gull.* Leeds: Peregrine Books. 268 pp.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.

FILCHAGOV, A.V. 1993. The Armenian Gull in Armenia. *British Birds* 86: 550–560.

FRECKLETON, R.P., HARVEY, P.H. & PAGEL, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160: 712–726.

GARLAND, T. & JANIS, C.M. 1993. Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *Journal of Zoology, London* 229: 133–151.

GARLAND, T. & IVES, A.R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* 155: 346–364.

GARLAND, T., HARVEY, P.H. & IVES, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41: 18–32.

GOETHE, F. 1937. Beobachtungen und Untersuchungen zur Biologie der Silbermöwe auf der Vogelninsel Memmersand. *Journal für Ornithologie* 85: 1–119.

GOODALL, J.D., PHILIPPI B., R.A. & JOHNSON, A.W. 1945. Nesting habits of the Peruvian Gray Gull. *Auk* 62: 450–451.

GÖTH, A. & EVANS, C.S. 2004. Egg size predicts motor performance and postnatal weight gain of Australian Brush-turkey (*Alectura lathami*) hatchlings. *Canadian Journal of Zoology* 82: 972–979.

GÖTMARK, F. 1984. Food and foraging in five European *Larus* gulls in the breeding season: a comparative review. *Ornis Fennica* 61: 9–18.

GRAFEN, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London B* 326: 119–156.

HAILMAN, J.P. 1967. The ontogeny of an instinct. The pecking response in chicks of the Laughing Gull (*Larus atricilla* L.) and related species. *Behaviour* 15 (Supplement): 1–159.

HARRIS, M.P. 1970. Breeding ecology of the Swallow-tailed Gull, *Creagrus furcatus. Auk* 87: 215–243.

HARRISON, C.J.O. 1975. A field guide to the nests, eggs and nestlings of European birds. London: Collins. 432 pp.

HARRISON, C.J.O. 1978. A field guide to the nests, eggs and nestlings of North American birds. London: Collins. 416 pp.

HARRISON, P. 1987. Seabirds of the world, a photographic guide. London: Christopher Helm. 317 pp.

HARVEY, P.H. & PAGEL, M.D. 1992. The comparative method in evolutionary biology. Oxford: Oxford University Press. 239 pp.

HIGGINS, P.J. & DAVIES, S.J.J.F. (Eds). 1996. Handbook of Australian, New Zealand and Antarctic birds. Vol. 3. Melbourne: Oxford University Press. 1028 pp.

KIRKHAM, I.R. & MORRIS, R.D. 1979. Feeding ecology of Ring-billed Gull (*Larus delawarensis*) chicks. *Canadian Journal of Zoology* 57: 1086–1090.

LACK, D. 1968. Ecological adaptations for breeding in birds. London: Methuen. 409 pp.

LIEBERS, D., DIERSCHKE, V. & DE KNIJFF, P. 2001. Genetic differentiation and phylogeography of gulls in the *Larus cachinnans-fuscus* group (Aves: Charadiiformes). *Molecular Evolution* 10: 2447–2462.

MARTINS, E.P. 2004. COMPARE, version 4.6b. Computer programs for the statistical analysis of comparative data. Bloomington, IN: Indiana University. [Available online at: http://compare.bio.indiana.edu/; accessed 28/01/09]

McKECHNIE, A.E., FRECKLETON, R.F. & JETZ, W. 2006. Phenotypic plasticity in the scaling of avian metabolic rate. *Proceedings of the Royal Society of London B* 273: 931–937.

McLACHLAN, G.R. & LIVERSIDGE, R. 1978. Roberts birds of South Africa. Cape Town: John Voelcker Bird Book Fund. 660 pp.

OLSEN, K.M. & LARSSON, H. 2004. Gulls of North America, Europe and Asia. Princeton and Oxford: Princeton University Press. 608 pp.

PARADIS, E., CLAUDE, J. & STRIMMER, K. 2004. APE: Analysis of Phylogenetics and Evolution in R language. *Bioinformatics* 20: 289–290. [Software available online at: http://cran.r-project.org/web/packages/ape/index.html; accessed 28/01/09]

PEDROCCHI, V., ORO, D. & GONZÁLEZ-SOLÍS, J. 1996. Differences between diet of adult and chick Audouin's Gulls *Larus audouinii* at the Chafarinas Islands, SW Mediterranean. *Ornis Fennica* 73: 124–130.

PÉREZ, C., LORES, M. & VELANDO, A. 2008. Availability of nonpigmentary antioxidant affects red colouration in gulls. *Behavioral Ecology* 19: 967–973.

PONS, J.M., HASSANIN, A. & CROCHET, P.A. 2005. Phylogenetic relationships within the *Laridae* (Charadriiformes: *Aves*) inferred from mitochondrial markers. *Molecular Phylogenetics and Evolution* 37: 686–699.

PURVIS, A. & RAMBAUT, A. 1995. Comparative Analysis by Independent Contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences* 11: 247–251.

REED, C.A. 1904. North American birds eggs. New York: Doubleday, Page and Co. 356 pp.

REEVE, J. & ABOUHEIF, E. 2003. Phylogenetic independence. Ver. 2.0. Montreal, QC: McGill University. [Available online at: http://biology.mcgill.ca/faculty/abouheif/protocols.htm; accessed 4 April 2009]

RICKLEFS, R.E. 1974. Energetics of reproduction in birds. In: Paynter, R.A. (Ed). Avian energetics. Cambridge, MA: Nuttall Ornithological Club. pp. 152–297.

TINBERGEN, N. & PERDECK, A.C. 1950. On the stimulus situation releasing the begging response in the newly hatched Herring Gull chick (*Larus argentatus argentatus* Pont.). *Behaviour* 3: 1–39.

URBAN, E.K., FRY, C.H. & KEITH, S. (Eds). 1986. Birds of Africa. Vol. II. London: Academic Press. 552 pp.

VELANDO, A. 2004. Female control in Yellow-legged Gulls: trading paternity assurance for food. *Animal Behaviour* 67: 899–907.

YORIO, P., BOERSMA, P.D. & SWANN, S. 1996. Breeding biology of the Dolphin Gull at Punta Tombo, Argentina. *Condor* 98: 208–215.