



Talas, L., Baddeley, R., & Cuthill, I. (2017). Cultural evolution of military camouflage. *Philosophical Transactions B: Biological Sciences*, 372(1724), [20160351]. <https://doi.org/10.1098/rstb.2016.0351>

Peer reviewed version

Link to published version (if available):  
[10.1098/rstb.2016.0351](https://doi.org/10.1098/rstb.2016.0351)

[Link to publication record in Explore Bristol Research](#)  
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via The Royal Society at <http://rstb.royalsocietypublishing.org/content/372/1724/20160351>. Please refer to any applicable terms of use of the publisher.

## University of Bristol - Explore Bristol Research

### General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:  
<http://www.bristol.ac.uk/pure/about/ebr-terms>

# Cultural evolution of military camouflage

Laszlo Talas<sup>1,2</sup>, Roland J. Baddeley<sup>2</sup> and Innes C. Cuthill<sup>1</sup>

<sup>1</sup> School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

<sup>2</sup> School of Experimental Psychology, University of Bristol, 12A Priory Road, Bristol BS8 1TN, UK

**Keywords:** military camouflage, defensive coloration, cultural evolution, texture analysis

*Submitted: 30 September 2016; Accepted 22 December 2016; Published 5 July 2017*

## Summary

While one has evolved and the other been consciously created, animal and military camouflage are expected to show many similar design principles. Using a unique database of calibrated photographs of camouflage uniform patterns, processed using texture and colour analysis methods from computer vision, we show that the parallels with biology are deeper than design for effective concealment. Using two case studies we show that, like many animal colour patterns, military camouflage can serve multiple functions. Following the dissolution of the Warsaw Pact, countries that became more Western-facing in political terms converged on NATO patterns in camouflage texture and colour. Following the break-up of the former Yugoslavia, the resulting states diverged in design, becoming more similar to neighbouring countries than the ancestral design. None of these insights would have been obtained using extant military approaches to camouflage design, which focus solely on concealment. Moreover, our computational techniques for quantifying pattern offer new tools for comparative biologists studying animal coloration.

## Introduction

At face value, the function of camouflage - whether in the natural world, in war, or in civilian contexts such as hiding security cameras or mobile phone transmitters - is straightforward: concealment. However, a striking feature of military camouflage is its diversity (figures 1-3). Within a single theatre of war, different nations, and even different units within the same army, employ markedly different solutions to concealment of the same objects, most obviously a human body. Why? We propose that the drivers of this cultural diversity mirror the forces at work in the evolution of colour in nature, but which are rarely considered in relation to camouflage, animal or military. Our paper has two goals. To illustrate the parallels between biological and cultural drivers of camouflage design, using one example of convergence and one of radiation. Second, and more generally applicable, to showcase a method for analysing the evolution, biological or

cultural, of a class of colour patterns that are widespread in nature and human design.

For centuries, military dress exhibited vivid colours to aid telling friend and foe apart on the battlefield [1-2]. It was not till the early 19th century that a concealing function for the colouration of uniforms was considered by national militaries. With the development of more accurate firearms, officers realised that the vivid colours previously used to recognise friendly troops now posed an easy target for enemy marksmen. In 1800, a British officer, Colonel Hamilton Smith, conducted a series of experiments to examine which colours fooled sharpshooters the best [3]. Under controlled lighting conditions, he ordered a group of rifleman to shoot targets painted in red, green or grey. He found that red targets were hit twice as often as grey, while green received an intermediate number of shots. Although he urged the British military to consider issuing grey uniforms for all infantry troops, it was not until half a century later that British forces began to wear less gaudy dress. In 1848, the Corps of Guides (a regiment of the British Indian Army) started to wear yellowish drab uniforms [4]. Termed 'khaki' in Hindustani, after the Persian word for 'soil', the dust-coloured uniforms gained quick popularity among troops and were adopted by all British foreign service in 1896, followed by the homeland army in 1902 [5]. Other nations, like the United States and Russia, also opted for khaki, while Germany updated its formerly blue uniforms to *Feldgrau* (field grey) in 1907 [6]. Despite heavy criticism, France retained a combination of dark blue coats with vivid red trousers, which were later blamed for heavy casualties in the early days of World War I, forcing France to issue less conspicuous "horizon blue" uniforms [7].

While World War I was the 'Cambrian explosion' for military camouflage - concealing canvas nettings, aircraft camouflage, dazzle colouration for ships were all invented during this war - uniforms remained relatively untouched. Only a handful of units, mainly snipers, started to use handmade camouflage dress. The first regular soldiers to receive officially issued camouflage clothing were the Italians in 1929 [8]. Designated as *M1929 telo*

*mimetico* (camouflage cloth), the pattern consisted of large chocolate-brown and pale green blotches on an ochre background. Germany and the Soviet Union soon developed their own patterns, followed by Hungary, the United Kingdom and the United States [8-9]. Camouflage uniforms became more commonplace in the frontlines of World War II and by the end of the Vietnam War, camouflage matured into a global phenomenon.

With minimising signal-to-noise ratio [10] being the new primary role of uniforms, their importance in identification has been largely forgotten. During the Normandy landings in 1944, the US Marines deployed a modified version of the camouflage pattern used successfully in the Pacific theatre. However, as it reportedly resembled German Waffen-SS patterns from a distance [11], it was quickly discarded and US troops reverted to standard Olive Green uniforms. In the 1970's, the geopolitical importance of the Middle East started to increase and several countries began to consider deploying camouflage specifically made for arid environments. The British design was also sold to the formerly allied Iraq [12]. This transaction resulted in an unfortunate situation ten years later at the onset of the Gulf War: British and Iraqi soldiers were wearing identical camouflage, which could have led to friendly fire. To avoid this, the British military was forced to rapidly replace its desert uniforms. These two examples illustrate that a failure to consider the recognition function of camouflage could have grave consequences.

Recently several militaries have issued patterns where subtle modifications undeniably create a distinctive national look. For example, Jordan and Croatia fielded uniforms (electronic supplementary material, figure S3) where a patch in the pattern resembles the outline of the country. The United Kingdom has recently adopted a variation of the globally successful MultiCam pattern [13], where the British military specifically requested inclusion of elements of the previous DPM (Disruptive Pattern Material) pattern to ease identification [14]. To our knowledge, this is the only example in the military literature (i.e. manuals and patents) where a pattern is explicitly designed to help soldiers recognise each other; most shifts concerning function beyond concealment are implicit and have not been scientifically validated. We consider two historical events, which had conspicuous impacts on the camouflage design of countries being involved in the dissolution of the Warsaw Pact (WP) and the break-up of Yugoslavia.

The Warsaw Pact (formally the Treaty of Friendship, Co-operation, and Mutual Assistance) was a defence treaty spearheaded by the Soviet Union to counter the NATO (North Atlantic Treaty Organisation) [15]. Initially incorporating seven East European countries plus the Soviet Union, the group remained a significant military alliance in Europe till 1991, when the Pact was disbanded. All non-Soviet members joined the NATO later, and

fielded new camouflage designs in the interim years.

The break-up of Yugoslavia resulted in new nations, which adopted various camouflage patterns for their forming militaries. These patterns were different from those of Yugoslavia, perhaps to signal their national identity. The two phenomena are comparable: break-up of a political union generating camouflage patterns. However, while our hypothesis is that former WP members converged on NATO designs, ex-Yugoslavian states radiated away from the camouflage of a single military.

Computer vision provides many generic ways of characterising visual patterns, but empirically we have found that they have three problems. First, their ability to describe all patterns comes at the cost of describing any given pattern well. Second, they are often chosen to be good measures for short distances (predicting, say, visual discriminability), but perform poorly over long distances. For instance, in a colour space based on the ability to discriminate, such as CIELab [16], all large colour distances are essentially equal [17]. Lastly, they often capture both important variation and variation that is an artefact of the data collection method or, a priori, irrelevant to the question at hand. We therefore argue it is important to develop visual pattern spaces that are optimised for the domain they will be applied to. We have previously, with colleagues, developed spaces based on reaction diffusion equations, and shown that they are very good at characterising single classes of visual textures: the coat patterns of felids [18] and snakes [19]. Here we propose a new pattern space that is appropriate for describing patterns formed by discrete patches (irregular blocks of a small number of colours). Many bird colours, for example, have such a structure [20]. We describe ways to characterize variations due to the pattern, the average colour and the distribution of colours separately. We then validate this space by using it to describe 610 military camouflage patterns; show that it provides a good characterisation of this space, and show that it is sensitive enough to capture the effects of two major "cultural environmental" effects: the dissolution of the Warsaw Pact [15, 21], and the break-up of Yugoslavia [22]. In both cases we find strong evidence in the pattern record for the influence of these two events, showing the sensitivity of the method. This potentially opens up the comparative method to a large number of other biological and cultural phenomena where the results of this "evolution" are well described by discrete patches of colour.

## Materials and methods

### *Image acquisition*

Images of camouflage uniforms were obtained from three sources: 585 from the private collection of

Brendan Conroy in Ireland (a significant international collector), 19 from the Museum of War History in Budapest, Hungary, and six from the collection of the authors. When available, more than one uniform with the same camouflage pattern was photographed, but only one image per pattern was selected for the final analysis. The criterion was simply the uniform in the best condition. Fading of uniforms is a potential problem, as some date back to the early 1930's. We only selected patterns with documented usage by camouflage collectors. In total, 610 unique patterns were included in the dataset. Some patterns were represented by replicas. Although it is debatable whether they are identical to their originals, the structural features and colours appear to be good matches to contemporary photographs and descriptions; hence we deemed them valid for comparison.

In order to establish an ancestral hierarchy between patterns (i.e. which pattern could have influenced another one), they need to be represented on a timeline. Temporal information (the year of issue or where available, the year of first testing) was acquired from manuals [23-28], patents [29-30], books [8-9, 31] and the International Camouflage Pattern Index [32]. More detail on photography and dating of camouflage is presented in the electronic supplementary material.

#### *Texture analysis*

Texture features were derived by convolving each image with a Log-Gabor filter bank created by the *gaborconvolve* [33] MATLAB [34] function. We used Log-Gabors rather than the more standard Gabors since they have a zero DC component, meaning that they do not respond to variations in the average signal level [35]. Having an image representation invariant to variations in luminance makes for a more robust characterisation. Log-Gabors have also been argued to better match both the statistics of natural images and the responses of early cortical cells [36] and are commonly used in describing textures with high accuracy, such as iris recognition [37] and fingerprint analysis [38]. After characterising the images with a Log-Gabor filter bank, we applied Principal Component Analysis to filter responses and used the Euclidean distance between the set of PC scores to derive a distance metric between patterns (figure 4) A detailed account of the texture analysis is provided in the electronic supplementary material.

#### *Colour analysis*

Following segmentation, the number of colours on an image was reduced by taking the segmented logical maps and calculating the median colour under the active area of each map. Although each image was selected to provide a representative sample of the whole pattern, the majority of images feature a smaller segment than the repeat size. Therefore, the colour proportions are only approximations of the original pattern descriptions. The next step was to represent each camouflage pattern in two colour spaces: average colour and a

quantised space where each pattern is represented by a histogram of their corresponding segmented colours. More detail on the colour analysis is presented in the electronic supplementary material.

#### *NATO convergence*

We selected 45 patterns from Bulgaria ( $n = 5$ ), Czechoslovakia ( $n = 11$ ), Hungary ( $n = 10$ ), Poland ( $n = 11$ ), and Romania ( $n = 8$ ) that were issued since 1949 (the foundation of NATO). Although Albania was a founding member of WP, it left the treaty in 1968 [15] and therefore we did not include Albanian patterns in the sample. East German patterns were not selected as it became part of the Federal Republic of Germany before the end of the WP. We also discarded all pixelated patterns from the analysis (see electronic supplementary material, figure S3 for examples). Pixelated patterns (commonly referred to as "digital" patterns) form a greatly distinctive group of camouflage uniform patterns. First fielded by Canada in 1996 and followed by the US Marines in 2001 [32], pixelated camouflage was rapidly adopted globally. As the pattern family originates from the NATO, without any previous history in uniforms, they could bias the analysis towards NATO-similarity. The test sample was then divided into two groups: patterns issued between 1949-1991, and since the dissolution of the Warsaw Pact in 1991. Two ancestral groups were defined: the first comprising all NATO patterns since 1949 ( $n = 105$ , from 15 countries) and the second containing all WP patterns between 1955 (the foundation of WP) and 1991 ( $n = 43$ ).

Each pattern in the test sample was then allocated to two ancestors, one from the NATO and one from the WP groups. Each ancestor pattern was defined as the pattern that was issued earlier and lay closest within the given distance space (texture, average colour, or quantised colour). Two distances were derived: one from the NATO ancestor ( $\Delta$ NATO) and one from the WP ancestor ( $\Delta$ WP). We then calculated a relative distance by dividing  $\Delta$ NATO with the sum of  $\Delta$ NATO and  $\Delta$ WP (figure 5). A value closer to zero mean that the pattern is closer to its NATO ancestor, while a value closer to one indicated a stronger WP association.

It is possible that former WP members updated their camouflage because NATO patterns simply offer better concealment and the change has little to do with signalling. Therefore, we created a "global" sample ( $n = 405$ , from 97 countries) comprising all post-1949 patterns except NATO and camouflage of the five East European countries in the test sample. Pixelated patterns were removed for the reason stated above. As with the test above, the global sample was split at 1991 and the same ancestral groups were used. If patterns all over the world have also become more NATO-like after 1991, then our 'NATO convergence' hypothesis for the changes in former WP countries would lose support.



The effects of splitting the sample into pre-1991 and post-1991 groups were analysed by fitting Linear Mixed Models using the lme4 package [39] in R [40]. Nested models were compared using the change in deviance on removal of a term and by the Bayesian Information Criterion [41]. Country of origin was treated as a random variable within the models. If a model including a term for category (pre-1991 or post-1991) had a significantly better fit to the one without it, the effect of the categorical separation was significant (e.g. the test sample patterns were significantly closer to NATO patterns than previous WP ancestors).

#### *Post-Yugoslavian radiation*

Thirteen patterns of Bosnia and Herzegovina ( $n = 3$ ), Croatia ( $n = 5$ ), Macedonia ( $n = 3$ ), and Slovenia ( $n = 2$ ) were chosen as the test sample. As with the previous analysis, we defined two ancestral groups. The first group contained Yugoslavian (later Serbian) patterns ( $n = 14$ ). The second group consisted of patterns issued by countries neighbouring the original Yugoslavia: Albania, Austria, Bulgaria, Greece, Hungary, Italy, and Romania ( $n = 47$ ). We chose these countries as their environments are comparable to those of Yugoslavia. Ancestors were chosen the same way as in the NATO convergence analysis, resulting in distances from each pattern in the test sample to the Yugoslavian ancestor ( $\Delta Yugo$ ) and to the neighbour ancestor ( $\Delta neighbour$ ). Relative distances were calculated by dividing  $\Delta Yugo$  with the sum of  $\Delta Yugo$  and  $\Delta neighbour$  (figure 6). If the camouflage of post-Yugoslavian states continued resembling Yugoslavian patterns, we expect a relative distance closer to zero. However, a relative distance at least 0.5 would suggest that the camouflage of post-Yugoslavian states does not resemble Yugoslavian patterns more than those of any nearby country, hence the possible association to Yugoslavian patterns is low. To test whether distances to Yugoslavian patterns are different compared to patterns of neighbouring countries, we fitted Linear Mixed Models using the same criteria for evaluation as above. Individual patterns in the test sample were treated as a random effect within the models in order to account for the paired design.

## Results

The first part of the analysis involved comparing the Bayesian Information Criterion (BIC) of a random effects model with a common country slope, but different intercepts to a model with varying slopes and intercepts. The former, simpler model was kept if it did not produce a poorer fit to the data, compared to the second, more complex model. All three simpler models for the 'NATO convergence' and the first two models (texture, average colours) for the 'Global sample' had lower BIC. The model with varying slopes for quantised colours in the 'Global sample' had a better fit than the one with common slopes, hence the former was selected. For the "Post-Yugoslavian radiation"

analysis it was not possible to fit a random effects model with varying slopes and intercepts as the number of observations ( $n = 26$ ) equalled the number of random effects. In this case, our initial models had a common slope, but different intercepts.

The selected models were then fitted to estimate the effect of category on relative distance by either including or removing this term (table 1). The category was a temporal division (pre-1991 vs. post-1991) for the 'NATO convergence' and 'Global sample' analyses, and ancestry (Yugoslavian vs. neighbours) for the 'Post-Yugoslavian' analysis. All models with category included produced a significantly better fit for 'NATO convergence' and 'Post-Yugoslavian radiation'. For 'Global sample', the effect of category was significant for average and quantised colours, but not for texture.

## Discussion

Our study has implications both for our understanding of how camouflage operates in a human military context, and for how to study this class of colour patterns in more general cultural and biological contexts. In animal camouflage, there is increasing evidence that colour patterns can serve multiple functions, such as concealment when viewed from afar but a warning signal close-up [42-44]. Our first case study shows that after the dissolution of the Warsaw Pact, the camouflage patterns of former members that were 'westward looking' moved closer to NATO patterns in all characteristics (texture, average colour and quantised colour; figure 5) compared to WP-era patterns. Interestingly, shifts towards NATO are already noticeable in 1989 and 1990, when revolutions against socialist regimes were happening in East Europe. Globally, textures of camouflage patterns did not become more NATO-like after 1991; suggesting that the post-WP shift cannot be solely explained by modernisation for a better pattern. On the contrary, both average and quantised colours moved towards NATO worldwide. Conflicts in more arid environments have been evident in the past 15 years (e.g. Afghanistan, Iraq), which is likely to be initially reflected in colour changes.

In our second case study, the post-Yugoslavian states changed their camouflage patterns (this of course can be seen with the naked eye, see figure 3), but our analysis shows that they retained little if any signature of the former state's pattern, becoming more similar to the camouflage of neighbouring states than that of the former Yugoslavia in texture, average colour and quantised colour (figure 6). The convergence of former Warsaw Pact countries on the camouflage of their new potential allies, and the radiation of the camouflage patterns of post-Yugoslavian states, indicates a signalling component to military camouflage. For these countries, the change of

camouflage maybe served primarily as a national statement *ex situ* (not on the battlefield), but camouflage can of course serve a recognition role in close encounters, paralleling the biological examples discussed earlier. Our method of analysis allows subtler signalling functions of camouflage to be revealed.

The texture analysis and average colour metrics can be applied to any pattern (e.g. [45]), but quantisation makes less sense for mottled patterns showing continuous gradations in colour. There are other powerful approaches to analysing colours [46-47] and patterns (obvious ones aimed at biological applications being [48-49]). We would argue that, for colours that are distinct and readily discriminable, Pele and Werman's approach [17] is better than that of Vorobyev and Osorio [47], which was designed to analyse near-threshold discrimination. However, it has the drawback, for biologists, of being designed around human vision. For texture, the methods of Endler [48] and Taylor et al. [49] are geometrical and statistical, so make no assumptions about the viewer's visual system, whereas ours is based on measures that have a more direct interpretation in terms of human perception.

In the case studies presented here, the control for non-independence of patterns was by a simple random effects model (post-Warsaw Pact changes) or pairwise comparison of before and after event (Yugoslavian radiation). Broader questions concerning the diversity of patterns require separation of signals of historical descent from local cultural 'adaptation' (e.g. most obviously to the environment, but also with respect to discrimination from potential enemies, etc.). As with the evolution of human language, such questions can be addressed using phylogenetically controlled comparative methods [50]. This has been met with resistance in some areas, but it is important to realise that the application of the statistical methods of evolution to cultural phenomena does not require the assumption that cultural change occurs by a similar mechanism [51]; the debate about whether there are cultural 'memes' analogous to genes [52-53] is orthogonal to the applicability of these reconstruction methods. Nevertheless, as with language and other cultural phenomena that exhibit quasi-Darwinian descent with modification, the pattern of relationships is not

a simple tree [51]. Camouflage and other modern human artefacts [54-56] exhibit not only horizontal transmission across lineages but the capacity to be influenced by any design in prior history. Traditional comparative approaches in biology assume a simple tree structure where every species has one, and only one, ancestor [57-58]. However, cultural artefacts, such as camouflage patterns, can have many 'parents'. For this reason, graph theoretical approaches [54, 56], also used in reconstruction of bacterial phylogenies [59-60], will be more appropriate. With the combination of new methods for network reconstruction, and new ways of quantifying complex patterns, we believe there are exciting new opportunities for the study of coloration in both nature and human culture, and establishing the parallels between them.

## Additional Information

### Acknowledgments

We thank Brendan Conroy and Tamás Baczoni for access to their uniform collections. We thank Tilo Burghardt (Computer Sciences, University of Bristol) and David Bull (Electrical & Electronic Engineering, University of Bristol) for discussions and advice on image processing, and Davide Pisani (Earth Sciences & Biological Sciences, University of Bristol) for discussions on graph theory methods for phylogenetic analysis. We thank Tim Caro, Will Allen, and an anonymous referee for their insightful comments that improved the manuscript.

### Supplementary Material

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.3738179.v2>.

### Data Accessibility

The dataset supporting this article is available on Dryad at <http://dx.doi.org/10.5061/dryad.n511h> [61].

### Authors' Contributions

I.C.C. devised the research topic; R.J.B. advised on and developed computational methods; L.T. did all the data collection and computation; all authors contributed to the interpretation of results and manuscript.

### Competing Interests

We have no competing interests.

### Funding

I.C.C. thanks the Wissenschaftskolleg zu Berlin for support during part of the study.

## References

1. Smith D, Black J, Kiley KF. 2009 *An Illustrated Encyclopaedia of Military Uniforms of the 19th Century*. Oxford: Anness Publishing.
2. Newark T. 2007 *Camouflage*. London: Thames & Hudson.
3. Lewis GG, Jones HD, Larcom TA, Williams J, Binney CR. 1853 *1853-1862, Aide-mémoire to the military sciences*. London: Weale.
4. Hodson-Pressinger S. 2004 Khaki uniform, 1848-49: first introduction by Lumsden and Hodson. *J. Soc. Army Hist. Res.* **82**, 341-347.
5. Newark T, Newark Q, Borsarello JF. 2002 *Brassey's Book of Camouflage*. London: Brassey's.
6. Somers J. 2006 *Imperial German Field Uniforms and Equipment 1907-1918*. Atglen: Schiffer Publishing.
7. Summer I. 2012 *They Shall Not Pass: The French Army on the Western Front 1914-1918*. Barnsley: Pen & Sword Military.
8. Borsarello JF. 1999 *Camouflage Uniforms of European and NATO Armies 1945 to the Present*. Atglen: Schiffer Publishing.
9. Desmond D. 1997 *Camouflage Uniforms of The Soviet Union and Russia 1937-To The Present*. Atglen: Schiffer Publishing.
10. Merilaita S, Scott-Samuel NE, Cuthill IC. 2017 How camouflage works. *Phil. Trans. R. Soc. Lon. B*, in press.
11. Blechman H, Newman A. 2004 *DPM*. London: DPM.

12. Hansard. H. C. Vol. 238, col. 383. (24 Feb 1994).
13. Crye Precision Ltd. 2016 MultiCam® Family of Camouflage Patterns [Internet]. Crye Precision Ltd. [cited 1 Dec 2016]. Available from: <http://multicampattern.com>
14. DSTL. 2014 *Testing the new Multi-Terrain Camouflage 2011* [Internet]. DSTL. [cited 1 Dec 2016] Available at: [http://www.dstl.gov.uk/news\\_events/press/pr2009/camouflage%20FINAL.pdf](http://www.dstl.gov.uk/news_events/press/pr2009/camouflage%20FINAL.pdf)
15. Reinalda B. 2010 *Routledge History of International Organizations*. Abingdon: Routledge.
16. CIE. 1986 *Publication CIE No. 15.2*. Vienna: Central Bureau of the CIE.
17. Pele O, Werman M. 2012 Improving perceptual color difference using basic color terms. *arXiv*, 1211.5556.
18. Allen WL, Cuthill IC, Scott-Samuel NE, Baddeley RJ. 2011 Why the leopard got its spots: relating pattern development to ecology in felids. *Proc. R. Soc. Lond. B*. **278**, 1373–80. (doi:10.1098/rspb.2010.1734)
19. Allen WL, Scott-Samuel NE, Baddeley RJ & Cuthill IC. 2013 The evolution and function of pattern diversity in snakes. *Behav. Ecol.* **24**, 1237–1250. (doi:10.1093/beheco/art058)
20. Stoddard MC, Prum RO. 2011 How colorful are birds? Evolution of the avian plumage color gamut. *Behav. Ecol.* **22**, 1042–52. (doi:10.1093/beheco/arr088)
21. Faringdon H. 1986 *Confrontation: The Strategic Geography of NATO and the Warsaw Pact*. Abingdon: Routledge & Kegan Paul.
22. Poirier CR. 1998 *The Breakup of Yugoslavia and the War in Bosnia*. Westport: Greenwood.
23. Baczoni T. 2000 *Terepszínek Magyarországon*. Budapest: Hadimúzeum Alapítvány.
24. Borsarello JF. 1989 *Camouflaged Uniforms of the Gulf & North African Forces*. Bromley: ISO-Galago Publications.
25. Borsarello JF, Palincx W. 2004 *Camouflage Uniforms of Asian and Middle East Armies*. Atglen: Schiffer Publishing Ltd.
26. Peterson D. 1995 *Waffen-SS Camouflage Uniforms and Post-War Derivatives*. Ramsbury: The Crowood Press Ltd.
27. Peterson D. 1995 *Wehrmacht Camouflage Uniforms & Post-War Derivatives*. Ramsbury: The Crowood Press Ltd.
28. Borsarello JF. 1989 *Camouflaged Uniforms of the Warsaw Pact & Non-Aligned Forces*. Bromley: ISO-Galago Publications.
29. Crye CC. 2012 *Textile with camouflage pattern*. US D659,4065.
30. Santos LDM, Townes DE, Patricio GR, Winterhalter CA, Dugas A, O'Neill TR, Lomba RA, Quinn BJ. 2004 *Camouflage US Marine Corps utility uniform: pattern, fabric, and design*. US 6,805,957 D.
31. Johnson RD. 1999 *Tiger Patterns*. Atglen: Schiffer Publishing Ltd.
32. Larson EH. 2009 *International Camouflage Pattern Index* [Internet]. International Camouflage Uniform Society. [cited 17 June 2016]. Available from: <http://camouflageindex.camouflagesociety.org/>
33. Kovasi P. 2013 *MATLAB and Octave Functions for Computer Vision and Image Processing* [Internet]. [cited 3 Feb 2015]. Available from: <http://www.peterkovasi.com/matlabfns/>
34. MATLAB and Statistics Toolbox Release 2014b, The MathWorks, Inc., Natick.
35. Fischer S, Šroubek F, Perrinet L, Redondo R, Cristóbal G. 2007 Self-Invertible 2D Log-Gabor Wavelets. *J. Comput. Vis.* **75**, 231–246. (doi:10.1007/s11263-006-0026-8)
36. Field DJ. 1987 Relations between the statistics of natural images and the response properties of cortical cells. *J. Opt. Soc. Am. A*. **4**, 2379–94. (doi:10.1364/JOSAA.4.002379)
37. Yao P, Li J, Ye X, Zhuang Z, Li B. 2006 Iris Recognition Algorithm Using Modified Log-Gabor Filters. In *ICPR '06 Proceedings of the 18th International Conference on Pattern Recognition Vol. 4*, 461–464. (doi:10.1109/ICPR.2006.726)
38. Wang W, Li J, Huang F, Feng H. 2008 Design and implementation of Log-Gabor filter in fingerprint image enhancement. *Pattern Recogn. Lett.* **3**, 301–308. (doi:10.1016/j.patrec.2007.10.004)
39. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
40. R Core Team. 2016 *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
41. Crawley MJ. 2007 *The R Book*. Chichester: John Wiley & Sons.
42. Barnett JB, Cuthill IC. 2014 Distance-dependent defensive coloration. *Curr. Biol.* **24**, R1157–8. (doi:10.1016/j.cub.2014.11.015)
43. Barnett JB, Scott-Samuel NE, Cuthill IC. 2016 Aposematism: balancing salience and camouflage. *Biol. Lett.* **12**, 10.1098. (doi:10.1098/rsbl.2016.0335)
44. Tullberg BS, Merilaita S, Wiklund C. 2005 Aposematism and crypsis combined as a result of distance dependence: functional versatility of the colour pattern in the swallowtail butterfly larva. *Proc. R. Soc. Lond. B*. **272**, 1315–21. (doi:10.1098/rspb.2005.3079)
45. Xiao F, Cuthill IC. 2016 Background complexity and the detectability of camouflaged targets by birds and humans. *Proc. R. Soc. Lond. B*. **283**, 20161527. (doi:10.1098/rspb.2016.1527)
46. Endler JA, Mielke PWJ. 2005 Comparing color patterns as birds see them. *Biol. J. Linn. Soc.* **86**, 405–31. (doi:10.1111/j.1095-8312.2005.00540.x)
47. Vorobyev M, Osorio D. 1998 Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B*. **265**, 351–8. (doi:10.1098/rspb.1998.0302)
48. Endler JA. 2012 A framework for analysing colour pattern geometry: adjacent colours. *Biol. J. Linn. Soc.* **107**, 233–53. (doi:10.1111/j.1095-8312.2012.01937.x)
49. Taylor CH, Gilbert FS, Reader T. 2013 Distance transform: a tool for the study of animal colour patterns. *Methods. Ecol. Evol.* **4**, 771–81. (doi:10.1111/2041-210X.12063)
50. Pagel M. 2009 Human language as a culturally transmitted replicator. *Nat. Rev. Genet.* **10**, 405–415. (doi:10.1038/nrg2560)
51. Gray RD, Greenhill SJ, Ross RM. 2007 The pleasures and perils of Darwinizing culture (with phylogenies). *Biol. Theory* **2**, 360–375. (doi:10.1162/biot.2007.2.4.360)
52. Dawkins R. 1976 *The Selfish Gene*. Oxford: Oxford University Press.
53. Lynch A. 1996 *Thought contagion. How Belief Spreads Through Society. The New Science of Memes*. New York: Basic Books.
54. Mesoudi A. 2011 *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences*. Chicago: University of Chicago Press.
55. Matthews LJ, Tehrani JJ, Jordan FM, Collard M, Nunn CL. 2011 Testing for divergent transmission histories among cultural characters: A study using Bayesian phylogenetic methods and Iranian tribal textile data. *PLoS ONE* **6**, e14810. (doi:10.1371/journal.pone.0014810)
56. Towner MC, Grote MN, Venti J, Borgerhoff Mulder M. 2012 Cultural macroevolution on neighbor graphs: Vertical and horizontal transmission among Western North American Indian societies. *Hum. Nat.* **23**, 283–305. (doi:10.1007/s12110-012-9142-z)
57. Freckleton RP, Harvey PH, Pagel MD. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726. (doi:10.1086/343873)
58. Harvey PH, Pagel MD. 1991 *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
59. Arnaud-Haond S, Moalic Y, Barnabe C, Ayala FJ, Tibayrenc M. 2014 Discriminating micropathogen lineages and their reticulate evolution through Graph Theory-based network analysis: The case of *Trypanosoma cruzi*, the agent of Chagas Disease. *PLoS ONE* **9**, e103213. (doi:10.1371/journal.pone.0103213)
60. Casgrain P, Legendre P, Sixou JL, Mouton C. 1996 A graph-theory method to establish serological relationships within a bacterial taxon, with example from *Porphyromonas gingivalis*. *J. Microbiol. Methods.* **26**, 225–236. (doi:10.1016/0167-7012(96)00911-6)
61. Talás L, Baddeley RJ, Cuthill IC. 2017 Data from: Cultural evolution of military camouflage. Data Dryad Repository. (<http://dx.doi.org/10.5061/dryad.n511h>)



## Figures and tables



**Figure 1.** Example camouflage patterns of four NATO members during the 1990's and early 2000's: *Centre Europe* (France), *Flecktarnmuster* (Germany), *DPM* (United Kingdom) and *M81 Woodland* (USA).

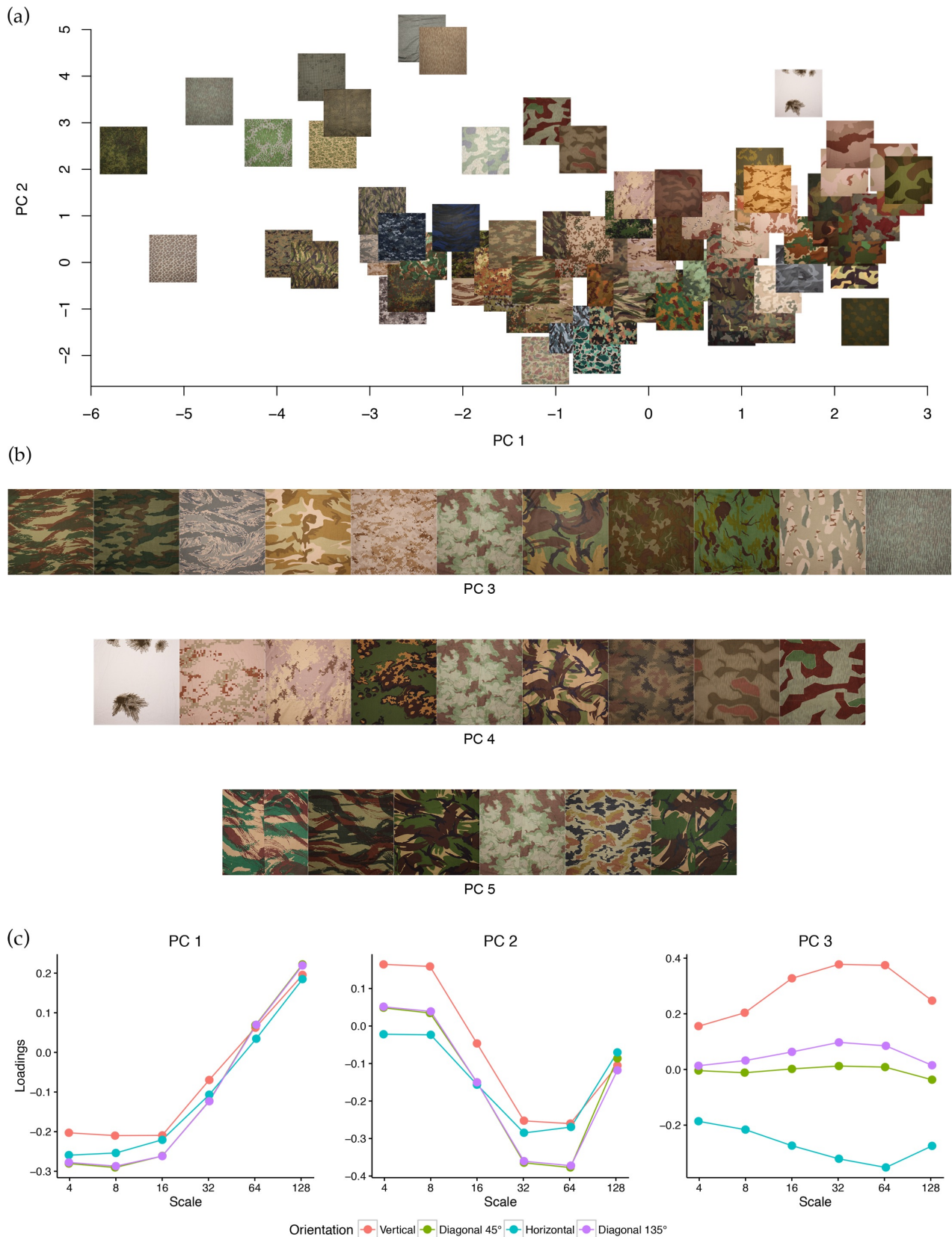


**Figure 2.** Example camouflage patterns of former Warsaw Pact members, which later became NATO members. Top row: pre-1991 patterns, bottom row: post-1991 patterns.  
\* dissolved into the Czech Republic and Slovakia after 1993.

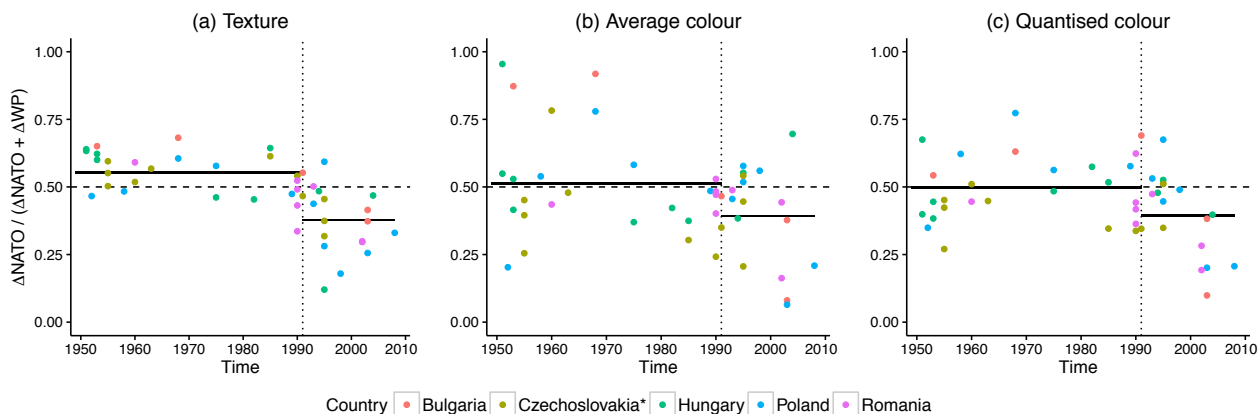


**Figure 3.** Example camouflage patterns from Yugoslavia and post-Yugoslavian states.  
\* became Serbia and Montenegro after 2003 and Serbia since 2006.

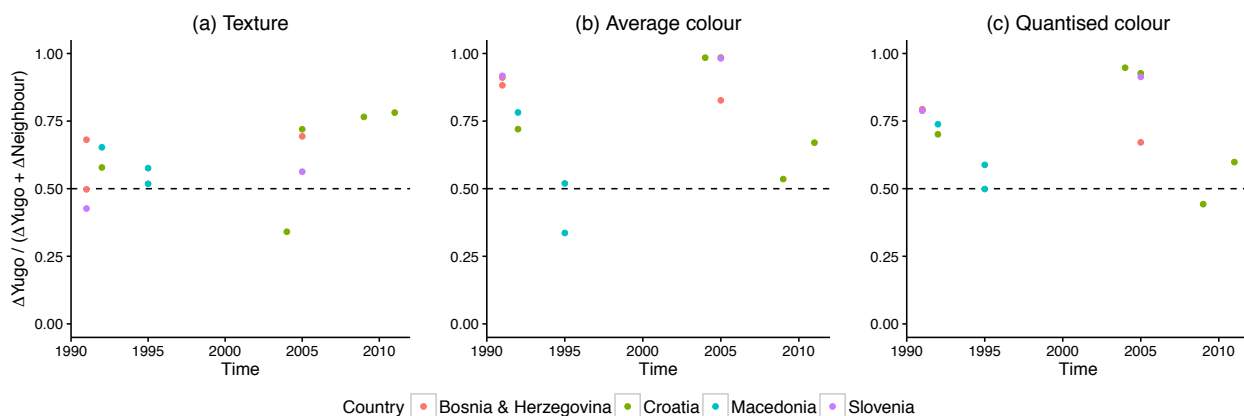




**Figure 4.** (a) Two-dimensional representation of the first two components in the texture space. For better intelligibility, not all patterns are plotted. (b) One-dimensional representations of the third, fourth, and fifth component. Images on the left are examples of low PC scores which increase by approximately one PC score towards the right. (c) Loadings of PCs plotted against spatial scale and orientation of Log-Gabor filters. The first component captures increasing spatial scale (i.e. overall 'size' of shapes), the second corresponds to the density of medium-sized (32 and 64 pixels) shapes on the pattern, while the third represents orientation (vertical vs. horizontal). The fourth and fifth components (not shown) account for the density of 16 and 32 pixel-sized shapes and left vs. right diagonal power, respectively.



**Figure 5.** NATO vs. WP relative distances plotted against time for the (a) texture, (b) average and (c) quantised colour analysis. Vertical dotted lines mark 1991, the year when the Warsaw Pact was dissolved. Horizontal solid lines represent the category means. Horizontal dashed lines are set to 0.5, where a pattern has the same similarity to both ancestral groups.



**Figure 6.** Relative distances of Yugoslavia vs. neighbouring countries plotted against time for the (a) texture, (b) average and (c) quantised colour analysis. Horizontal dashed lines are set to 0.5, where a pattern has the same similarity to both ancestral groups.

**Table 1.** Comparison of linear mixed models with and without the category term.

		BIC (without)	BIC (with)	Estimate	SEM	$\Delta$ deviance	d.f.	<i>p</i>
<b>NATO convergence</b>	texture	-38.451	-55.64	-0.1757	0.0346	21.04	1	< 1e-5
	avg. colours	-9.891	-10.609	-0.1206	0.0563	4.567	1	0.0326
	quantized colours	-38.542	-41.071	-0.1058	0.0404	6.379	1	0.0116
<b>Global sample</b>	texture	-539.44	-533.88	-0.0066	0.0124	0.59	1	0.5961
	avg. colours	-459.96	-462.04	-0.0378	0.0133	8.09	1	0.0045
	quantized colours	-653.42	-659.09	-0.0416	0.0121	23.68	1	< 1e-4
<b>Post-Yugoslavian radiation</b>	texture	113.02	107.62	1.8315	0.5539	8.65	1	0.0033
	avg. colours	16.531	13.719	0.2515	0.1001	6.0702	1	0.0138
	quantized colours	5.8563	-2.183	0.2662	0.0737	11.297	1	0.0008