

Why the leopard got its spots: relating pattern development to ecology in felids

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A complete explanation of the diversity of animal colour patterns requires an understanding of both the developmental mechanisms generating them and their adaptive value. However, only two previous studies, which involved computer-generated evolving prey, have attempted to make this link. This study examines variation in the camouflage patterns displayed on the flanks of many felids. After controlling for the effects of shared ancestry using a fully resolved molecular phylogeny, this study shows how phenotypes from plausible felid coat pattern generation mechanisms relate to ecology. We found that likelihood of patterning and pattern attributes, such as complexity and irregularity, were related to felids' habitats, arboreality and nocturnality. Our analysis also indicates that disruptive selection is a likely explanation for the prevalence of melanistic forms in Felidae. Furthermore, we show that there is little phylogenetic signal in the visual appearance of felid patterning, indicating that camouflage adapts to ecology over relatively short time scales. Our method could be applied to any taxon with colour patterns that can reasonably be matched to reaction–diffusion and similar models, where the kinetics of the reaction between two or more initially randomly dispersed morphogens determines the outcome of pattern development.

Keywords: camouflage; background matching; pattern formation; reaction–diffusion models; melanism; disruptive selection

1. INTRODUCTION

The patterns displayed on the flanks of felids are intriguing in their variety. Previous studies of the adaptive function of cat coat patterns have indicated that they are likely to be for camouflage rather than communication or physiological reasons [1,2]. The primary hunting strategy of felids is to stalk prey until they are close enough to capture them with a pounce or quick rush [3,4]. As hunts are more successful when an attack is initiated from shorter distances [5,6], cats benefit from remaining undetected for as long as possible and camouflage helps achieve this. Many smaller cats are also likely to be camouflaged for protection from predation [7].

Two studies have previously examined felid patterning using the comparative method. Ortolani & Caro [1] used a concentrated changes test [8] to find a significant association in felids between losing spotted coats and absence from forested environments. Across all carnivores, this association between spots and forested habitats approached significance and spots were significantly associated with arboreality. Similarly, Ortolani [2] found support for dark spots on carnivores being associated with closed habitats, arboreal locomotion and preying on ungulates. In the study of Ortolani & Caro [1], there was no association between vertically striped coats and utilization of grassland habitats in either felids or all carnivores. There was some support for vertical

stripes emerging in species using grasslands and terrestrial locomotion when examining all carnivores in the more extensive dataset used by Ortolani [2], perhaps due to greater statistical power, as well as for an association between dark horizontal stripes and arboreal locomotion. Overall, their results supported the hypothesis that felid flank patterns evolve to match the visual appearance of the background.

Ortolani & Caro [1] were aware that their method of subjective classification of patterning as either uniform, spotted, horizontally or vertically striped may have masked important variety in felid patterning (so reducing statistical power). Twenty-two of 32 felids were classed as spotted, six as uniform, two as horizontally striped and two as vertically striped. Classifying patterns into broad categories was a necessity in an expansive study that examined all carnivores. In this study, we develop a parametric classification method that describes detailed differences in the visual appearance of markings displayed by, for example, jaguars *Panthera onca*, clouded leopards *Neofelis nebulosa* and serval *Caracal serval*—three species with very different appearances that were all classed as spotted under previous classification schemes [1,2].

Increasingly, studies of animal patterning have used image processing techniques such as Fourier analysis [9], wavelet analysis [10], edge detection [11], and combinations of these and similar techniques [12] to obtain statistics that quantify aspects of patterning. However, such methods rely on obtaining standardized and calibrated images [13]. With often rare, secretive and exotic animals as our subject, we utilized the large corpus of

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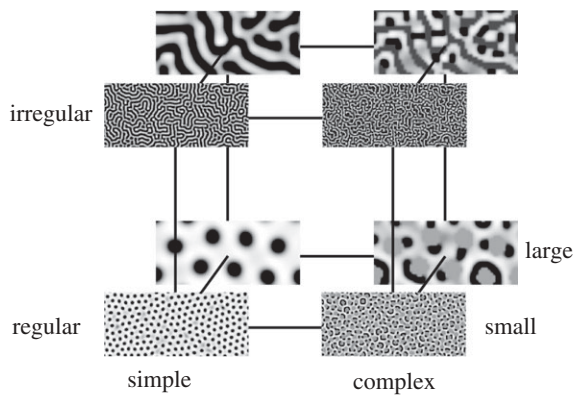


Figure 1. Visualization of camouflage space. Observers were able to select a reaction–diffusion comparison pattern from a point in this space that they judged most closely approximated the standard felid flank pattern displayed adjacently. Two other dimensions—pattern anisotropy and probability of patterning—are not shown. For details of how the dimensions were specified see §2.

images available on the Internet. Such images vary in many ways (including scale, viewpoint, lighting conditions, and camera hardware and set-up) and may contain features such as occlusions and shadows, the effects of which are very difficult to discount using image processing techniques. Human observers, however, find it very easy to ignore task-irrelevant information. Although human judgements may be unsuitable for colour analysis (since colour perception varies strongly between species), the fundamentals of shape and pattern perception are likely to be similar for humans and felids' predators and prey [14,15].

The method used in this study is inspired by reaction–diffusion theories of biological pattern formation. Although the mechanism of felid pattern development is not yet known [16,17], reaction–diffusion models represent a good candidate [18,19] and, crucially for our goal of parametric pattern description, can form patterns very similar to those observed in felids and many other taxa [18–21]. Previously, only Bond and Kamil [22,23] have linked the utility of different camouflage patterns to developmental mechanisms that can generate pattern variety. They used a genetic algorithm to evolve patterns on reproducing populations of artificial 'moths' under predation by blue jays. Linking development, mechanism, function and phylogeny offers a complete explanation of pattern variety [24]. It is also important as developmental mechanisms may constrain the range of pattern phenotypes.

The reaction–diffusion patterns can be manipulated along several dimensions that together can be thought of as comprising felid 'camouflage space' (figure 1). Human observers classified standard examples of felid flank patterns to the closest matching comparison pattern in this multidimensional space. The values of variables in the underlying equation that generated the chosen pattern and distribution of observers' classification decisions parameterize the important properties of each standard image. The five dimensions can be conceptualized as: (i) patterned versus plain, (ii) pattern irregularity, (iii) pattern complexity, (iv) pattern element size and (v) the anisotropy (directionality) of pattern elements. These

measures were then tested for relationships with ecological variables that have previously been proposed to drive the evolution of pattern phenotypes, including habitat, locomotion, activity time, social systems, prey size, body size and weight. We also collected information on the prevalence of melanism in each species to test predictions made by alternative theories for the prevalence of melanistic polymorphs in some species of Felidae. Disruptive selection can cause polymorphism when extreme morphs gain benefits. This is more likely in species with broad ecological niches, as variable environments offer more opportunities that unusual morphs could potentially exploit [25]. Apostatic selection, where unusual variants benefit because they are less familiar to predators and prey, would be the likely mechanism if melanism were more common in diurnal species, when visual search images would be of greater importance.

2. MATERIAL AND METHODS

(a) Image acquisition and selection

We collected images of 35 species of Felidae from the Internet. The search was conducted using Google Image Search and various wildlife photography resources such as Arkive (www.arkive.com) using scientific and all common names as search terms. Initially all available non-duplicate images that could be reliably identified as containing an example of a specific non-domestic felid species were collected. From each species's image corpus the six 'best' images were selected: better images contained the subject posing in profile with the side of the animal in full view, free from distortions and occlusions. They were also in focus and taken in natural lighting conditions and dry weather. Images with a large number of pixels were preferred. In a very few instances, particularly for very rare or otherwise difficult to photograph cats, such as those living in rainforests, we were unable to obtain six images without making some concessions to quality. However, in no instance was the shape or size of any coat pattern elements unclear, although colour balance, saturation and contrast all may have had some effect on the visual perception of any pattern. By avoiding photographs taken in the same image set, we reduced the chances that an individual animal was represented more than once. In species with pattern polymorphism no attempt was made to select photos with particular variants, but images of melanistic individuals were excluded. We only used images of adult individuals, although it should be noted that a number of species such as puma *Puma concolor*, lion *Panthera leo* and cheetah *Acinonyx jubatus* undergo ontogenetic change in patterning that may well be adaptive.

To obtain approximately orientation-invariant images of the body patterns, we took rectangular crops from the selected images using the base of the neck and tail as the x -axis start and end points, with the length of the y -axis being specified by the distance to the highest part of the underside (which was typically just behind the front legs). Bilinear interpolation was used to rotate the off-cardinal crop area to cardinal axes. Crops were then resized to 228×128 pixels to obtain approximately scale-invariant standard images of each species. An example of the images and crops for a single species are available in the electronic supplementary material. All image processing was done using MATLAB R2009b with the Image Processing Toolbox (The Mathworks Inc., MA, USA).

(b) Reaction–diffusion pattern creation

The patterns were created according to the equations described by Bard & Lauder [26] and Lauder [27], which were able to generate the range of patterns we were interested in. Full details are given in the electronic supplementary material. Simple patterns were created with all parameters fixed except the diffusion speed of one of the two morphogens (*Db*). Lower diffusion rates create patterns with more irregular pattern elements; higher values create patterns with more regular spots.

Complex patterns were created following the cascade method described by Turk [20]. This involves fixing morphogen concentrations of the simple patterns in areas where patterning has already formed and then resuming the reaction–diffusion process. New pattern elements form around the existing pattern elements.

The comparison patterns presented to observers consisted of the concentration of chemical *b* at each point in the 288×128 pixel central area displayed as a greyscale image after being scaled by subtracting the minimum concentration then dividing by the maximum concentration.

(c) Classification task

The classification task was programmed in MATLAB on a PC, using Matlab's GUI programming tools. Observers were able to interactively select, display and manipulate the reaction–diffusion comparison patterns until they confirmed that they were satisfied they had achieved a good match with the standard image pattern. Full details and screenshots of the classification utility are available in the electronic supplementary material and the utility is available on request from the corresponding author.

(d) Observers and classification procedure

Five observers performed the classification task: one was an author (W.L.A.) and four were naive observers. All had normal or corrected-to-normal visual acuity. They were instructed to match the visual appearance of any patterning on the standard image to the comparison pattern as closely as possible within a reasonable period of time, ignoring incidental features such as occlusions or shadows. An experimenter then demonstrated how to manipulate the comparison pattern and showed them the range of patterns available to them.

(e) Collection and coding of felid trait information

Data were collected independently of previous comparative studies of felid coloration. Principle sources of information included the works of Kitchener [28], Nowack [29], Macdonald [30] and Sunquist & Sunquist [31]. On the few occasions where information from different sources conflicted, an additional independent source was consulted for verification. When this was not possible, the most recent information was used. How traits were coded depended on the precision of information available. For example, our locomotion trait would ideally be the percentage of activity time each cat spent in trees, but these data were unavailable. The precision of available data enabled us to place each species in one of five ordered categories: terrestrial; terrestrial and occasionally arboreal; terrestrial and arboreal; arboreal and occasionally terrestrial; and arboreal. Similarly, activity time was coded as: nocturnal; mainly nocturnal and/or crepuscular; no activity time preference; mainly diurnal; and diurnal. Body length and weight were coded as the mean of the minimum and maximum values published by Sunquist & Sunquist [31]. We used the information in

Meachen-Samuels & Van Valkenburgh [32] to classify each species's prey size as small, medium or large. The information in the works of Sunquist & Sunquist [31] and Robinson [33] enabled us to identify whether melanism was common, rare or absent in each species. Sociability was recorded as a binary trait with species known (at least in some instances) to live in pairs or any greater level of intraspecific non-reproductive interaction being classed as sociable.

Each species was coded as being absent (0), sometimes present (0.5) or preferentially present (1) in several habitat categories: boreal and coniferous forest; temperate forest; tropical forest; riparian zones (together classed as closed environments); grasslands and plains; desert and semi-desert; and mountainous and rocky regions (classed as open environments). To account for the greater importance of the properties of habitat-to-habitat specialists (e.g. Andean mountain cats *Leopardus jacobita*) than more generalist cats (e.g. puma *Puma concolor*), these scores were then normalized by the sum of all habitat scores for each species. Thus, the coding of a cat found in only one habitat would remain unchanged as it should be strongly adapted to this habitat type, while the normalized score would be lower for a cat found in the same habitat and also several others. The amount each score had to be normalized by also gives an index of how habitat specialist or generalist each cat is. We do not know whether generalist cats are adapted to one of their several habitats in particular, or whether patterning reflects a compromise camouflage solution to all the habitats each is found in [34]. We also created a summary variable to capture each species's overall preference for open or closed environments by dividing the sum of open habitat scores by the sum of all habitat scores. The classifications of ecological variables are available as electronic supplementary material and were broadly comparable to Ortolani & Caro [1] and Ortolani [2], with a few minor differences probably caused by the different coding schemes and recent insights into felid ecology.

(f) Statistical methods

Probability of patterning and probability of complex patterning were the fraction of all comparison patterns for each species classified by all observers as patterned and complexly patterned, respectively. The diffusion speed of morphogen *b* (*Db*) and the *x*- and *y*-axis stretch for each species were recorded as the median value of all patterned classifications. The *x*-axis stretch was then adjusted to compensate for distortions introduced if the original image was stretched to present it at the fixed aspect ratio. Pattern anisotropy was taken as the *x*-axis stretch divided by *y*-axis stretch, logged. Pattern elements were assumed to be elliptical when calculating their area relative to body size from the *x*- and *y*-axis stretch. A species's pattern size in absolute terms was calculated by multiplying the *x*- and *y*-axis stretch by the size ratio between the species and the smallest felid (the rusty-spotted cat *Prionailurus rubiginosus*) before calculating the ellipse area.

As all the variables collected were continuous or quasi-continuous, we used a generalized least-squares approach for the comparative analysis [35]. We estimated lambda (λ), a measure of the phylogenetic signal present in the residuals of each comparison [36,37], and used it to adjust shared branch lengths appropriately before using linear regression to test each relationship of interest. The analysis was performed using the `pglmEstLambda` function in the R implementation of CAIC [38–40] (<https://r-forge.r-project.org/projects/caic/>). We used the molecular phylogeny

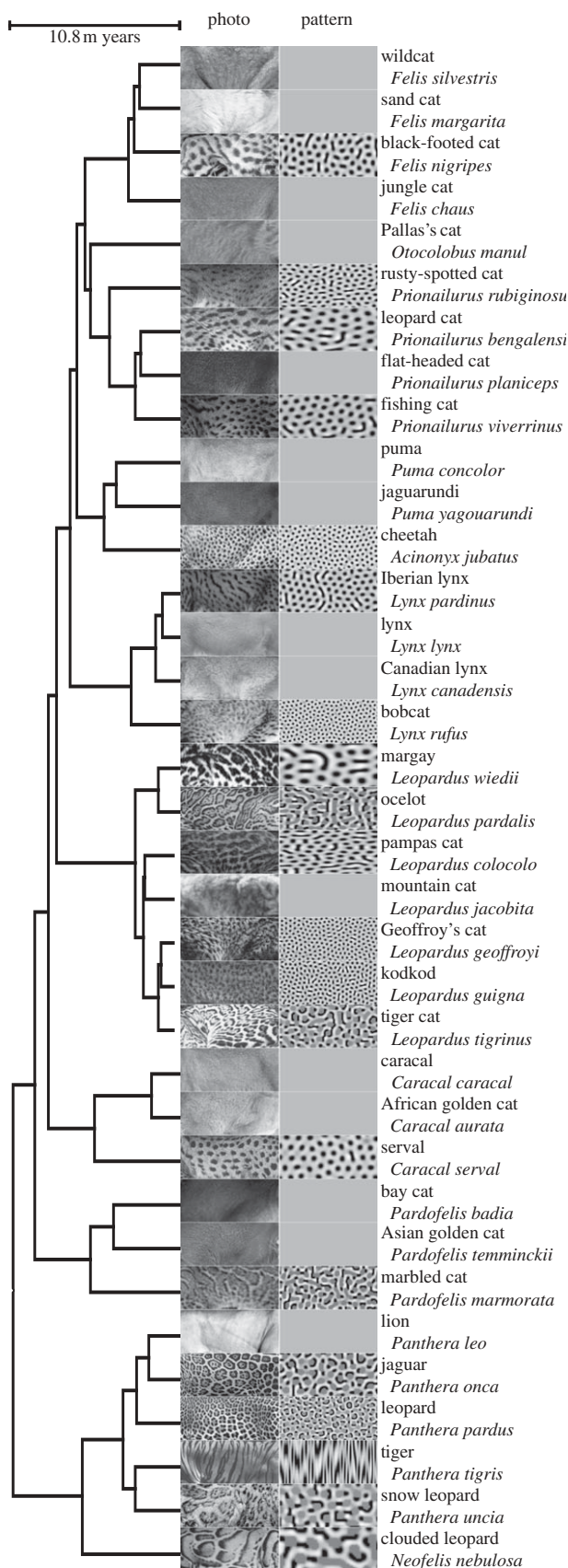


Figure 2. Synthesized patterns using median classification values for each species traced over the phylogeny used to control for potential statistical non-independence of data points in the analysis [41]. For each species we first calculated whether the median pattern classification (by all observers and all example patterns) was plain or patterned. If the species was on average patterned, for all patterned classifications we calculated the median values of Db , pattern

reported by Johnson *et al.* [41] and updated in the works of Driscoll *et al.* [42] and Werdelin *et al.* [43], as it is fully resolved with high support and includes branch length information.

3. RESULTS

Classification was highly consistent, with intraclass correlation coefficients [44] of the observers' judgements ranging from 0.94 to 0.98 for each of the measures. The scores of W.L.A. were well clustered with those of the other (naive) judges. Single classifications by single observers (resulting in 0.03 or 0.97 probability of patterning for Pallas's cat *Otocolobus manul*, and marbled cat *Pardofelis marmorata*) were considered as mistakes and removed from the analysis. Nine of the 35 cats were always classified as plain, 16 as always being patterned and 10 showed some variability, mainly relating to pattern polymorphism. Four of the patterned cats were always judged to have complex patterns, with eight other species occasionally being classed as complex (figure 2; electronic supplementary material). The 10 per cent of jaguarundi *Puma yagouarundi* images classified as patterned were found to be outliers in pattern space (see electronic supplementary material), showing a fine-grained low-contrast pattern, clearly an attempt by observers to capture the texture of reflected light off textured dark fur. As this texture may well be non-incidental, we saw no reason to exclude these results from analysis of patterning of any kind, although as the mechanism creating this pattern is clearly not the same as for other examples we excluded the jaguarundi from analysis of the particular kind of pattern.

Patterning of any kind was associated with closed environments ($n = 35$, $\lambda < 0.01$, $r^2 = 0.12$, $\beta = -0.28$, $t = 2.09$, $p = 0.045$). Cats found in the open were more likely to be plain, especially those found in mountainous regions ($n = 35$, $\lambda < 0.01$, $r^2 = 0.12$, $\beta = -0.16$, $t = 2.13$, $p = 0.04$). The particular kind of pattern was important too: looking at the species that were classified as being at least sometimes patterned, cats with stronger preferences for tropical forest habitat exhibited more irregular patterns ($n = 25$, $\lambda < 0.01$, $r^2 = 0.18$, $\beta = -0.13$,

stretch along the x - and y -axes, and whether they were on average classed as simple or complex patterns. Numerical data are available in the electronic supplementary material. These values were used to synthesize new patterns using the processes described in §2*b*. The photos on the left are examples for reference of the standard images used in the classification task. Written permission has been sought for the use of all copyright images. We would like to thank Márcio Cabral de Moura (jaguar), Gerald Cubitt (clouded leopard), Francisco Erize (Geoffroy's cat), Mark Deeble and Victoria Stone/www.osfimages.com (serval), Colin Groves (tiger), Joachim S. Müller (Asian golden cat), Nerdybirders.com (jungle cat), Tony Rath (pampas cat), T. J. Rich/naturepl.com (caracal), Jurgen and Christine Sohns/www.flpaimages.co.uk (jaguarundi), Terry Whittaker (rusty-spotted cat), Art Wolfe/www.artwolfestock.com (bay cat) and Günter Ziesler (margay).

Table 1. Estimates of phylogenetic signal (λ) present in characters. Characters not significantly different from $\lambda = 0$ have no detectable phylogenetic component to character variation. Characters not significantly different from $\lambda = 1$ fit stochastic (e.g. Brownian motion) models of character evolution along the phylogeny; the trait covaries between species in direct proportion to their shared evolutionary history [38].

character	λ	maximized log-likelihood	maximized log-likelihood ($\lambda = 0$)	maximized log-likelihood ($\lambda = 1$)
probability of patterning	0.04	-20.84	-20.86 ^a	-25.19**
pattern irregularity (<i>Db</i>)	<0.01	-35.41	-35.41 ^a	-39.09**
probability of complex patterning	0.49	-9.70	-12.43*	14.90**
pattern size relative to body size	1.00	-30.94	-34.91**	-30.94 ^a
absolute pattern size	1.00	-30.51	-34.90**	-30.51 ^a
pattern anisotropy	0.18	1.01	0.69 ^a	-1.20*
prevalence of melanism	<0.01	-17.50	-17.50 ^a	-20.09*
open habitat preference	<0.01	-13.91	-13.91 ^a	-19.55**
temperate forest	<0.01	12.29	12.29 ^a	7.92**
tropical forest	0.41	-5.13	-5.59 ^a	-8.89*
coniferous forest	<0.01	17.02	17.02 ^a	7.43***
riparian habitats	<0.01	12.03	12.03 ^a	3.34***
grasslands and plains	<0.01	7.05	7.05 ^a	-3.62***
mountains	<0.01	5.87	5.87 ^a	-3.67***
desert and semi-desert	0.24	5.87	4.92 ^a	2.41*
sociability	<0.01	-22.76	-22.75 ^a	-29.79***
activity time	0.79	-48.25	-49.30 ^a	-49.45 ^a
locomotion	0.71	-51.17	-53.70*	-52.59 ^a
prey size	0.53	-38.75	-41.81*	-42.89**
average weight (normalized)	0.74	-41.83	-49.62***	-42.25 ^a
average length (normalized)	1.00	-37.99	-49.62***	-37.99 ^a

^aNot significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

$t = 2.26$, $p = 0.034$). This may be the case for closed environments in general ($n = 25$, $\lambda < 0.01$, $r^2 = 0.27$, $\beta = 0.13$, $t = 2.05$, $p = 0.051$). Complex patterns were predicted by preference for closed environments ($n = 25$, $\lambda < 0.01$, $r^2 = 0.18$, $\beta = -0.36$, $t = 2.21$, $p = 0.037$), and tropical habitats in particular ($n = 25$, $\lambda < 0.01$, $r^2 = 0.21$, $\beta = 0.33$, $t = 2.37$, $p = 0.026$). There was also a suggestion that patterned cats found on grasslands and plains were likely to have simple patterns ($n = 25$, $\lambda < 0.01$, $r^2 = 0.15$, $\beta = -0.19$, $t = 2.04$, $p = 0.052$).

Species' behaviour also predicted aspects of patterning. The more time cats spent in trees, the more likely they were to be patterned ($n = 35$, $\lambda = 0.70$, $r^2 = 0.17$, $\beta = 0.94$, $t = 2.63$, $p = 0.013$), especially with irregular ($n = 25$, $\lambda < 0.01$, $r^2 = 0.20$, $\beta = -0.14$, $t = -2.40$, $p = 0.025$) and complex patterns ($n = 25$, $\lambda < 0.01$, $r^2 = 0.18$, $\beta = 0.35$, $t = -2.21$, $p = 0.037$). These relationships may reflect the greater incidence of arboreal locomotion in more densely vegetated habitats ($r^2 = 0.44$, $p = 0.0002$), though perhaps arboreal forest habitats have particularly variable texture compared with terrestrial forest habitats. More nocturnal activity patterns were unrelated to the likelihood of a species being patterned ($n = 35$, $\lambda = 0.82$, $r^2 = 0.03$, $\beta = -0.35$, $t = -1.00$, $p = 0.322$) but, among patterned cats, those with irregular patterns were more likely to be more active at night ($n = 25$, $\lambda < 0.01$, $r^2 = 0.20$, $\beta = 0.42$, $t = 2.40$, $p = 0.024$).

We found no evidence of pattern anisotropy in horizontal or vertical orientations, or the size of pattern elements relative to body size or in absolute terms, being associated with any particular habitats or

behaviours. Nor was prey size associated with any particular aspect of patterning, and there was no evidence for a relationship between the sociability of cats and any of the pattern measures, consistent with our assumption that the flank markings of cats are not related to social signalling.

Examining estimates of λ for each character (table 1) and tracing patterning over the phylogeny (figure 2) indicates that patterning emerges or disappears frequently. The same is true of the irregularity of patterning and, to a lesser extent, the complexity of patterning (which is concentrated in the big cat, bay cat and ocelot lineages). This indicates that many aspects of patterning in Felidae are evolutionarily labile. Similarly, λ does not differ significantly from 0 for all habitat traits, suggesting that felids have radiated rapidly to fill new and diverse niches. Activity time and locomotion are more conservative and, as previous studies have shown, λ reliably characterized traits known to be conserved along phylogenies such as body length and weight [37].

We found good support for disruptive selection explaining the prevalence of melanism in felids; melanism was more common in cats with stronger preferences for temperate forests ($n = 35$, $\lambda = 0.58$, $r^2 = 0.35$, $\beta = 0.26$, $t = 4.22$, $p < 0.0001$), which seasonally vary, but no other habitats; it was also more prevalent in more habitat generalist cats ($n = 35$, $\lambda = 0.34$, $r^2 = 0.24$, $\beta = -0.26$, $t = 3.20$, $p = 0.003$). We also constructed measures that captured species' flexibility in activity time, locomotion strategy and lighting environment from the absolute value of species' scores subtracted from the category median (diurnal and nocturnal activity time, terrestrial

and arboreal locomotion, and the lighting environment score when preference for open and closed environments was equal). Melanism was more common when cats were diurnally and nocturnally active rather than diurnal or nocturnal ($n = 35$, $\lambda = 0.04$, $r^2 = 0.25$, $\beta = -0.79$, $t = 3.29$, $p < 0.0001$), and when they used terrestrial and arboreal locomotion rather than one locale ($n = 35$, $\lambda = 0.28$, $r^2 = 0.19$, $\beta = -0.78$, $t = 2.80$, $p < 0.008$). However, there was no evidence that melanism was more prevalent in cats that used both open and closed environments rather than just one or the other ($n = 35$, $\lambda < 0.01$, $r^2 = 0.04$, $\beta = -0.10$, $t = 1.22$, $p = 0.23$). The apostatic selection hypothesis was poorly supported; it predicts none of the relationships mentioned and there is little support for a relationship between melanism and diurnal activity when visual novelty should be more advantageous ($n = 35$, $\lambda = 0.66$, $r^2 = 0.07$, $\beta = 0.61$, $t = 1.58$, $p = 0.12$).

4. DISCUSSION

These findings support the hypothesis that felid flank patterns function as background matching camouflage. Evolution has generally paired plain cats with relatively uniformly coloured, textured and illuminated environments, and patterned cats with environments 'full of trees and bushes and stripy, speckly, patchy-blatchy shadows' [45]. It is also likely that the particular pattern generally evolves to resemble the size, shape and variability of pattern elements in the background [46]. Cats using closed environments and arboreal locomotion are more likely to have complex patterns than those that use open habitats and terrestrial locomotion. Especially irregular patterns have evolved on more nocturnal hunters, those found in tropical forests and those that hunt in trees. Although we have not quantified the visual appearance of the background in this study, it is reasonable to assume that closed environments, especially tropical forests and arboreal habitats, have a more irregular and complex texture than open environments owing to the structure of the elements they contain, their configuration and density, and how they interact with light and cast shadows [46].

Like Ortolani & Caro [1], we found no support for the proposition that vertical stripes are associated with grasslands: only the tiger was classified as having vertically elongated patterns and it is not strongly associated with this habitat. While tigers may be very well camouflaged, and their habitats may have more spectral power at vertical orientations [9], this raises the question of why vertical stripes are not more common in felids and other mammalian taxa.

We observed strong associations which suggest that disruptive selection is the mechanism accounting for the prevalence of melanistic forms in some cats but not others. It is unclear how melanistic forms might use their environments differently from standard morphs although they would be expected to be found at the extremes (for example having especially nocturnal activity patterns or living in particularly dense forest).

Plotting species' positions in camouflage space shows that some cats are intriguing camouflage outliers. Cheetahs *Acinonyx jubatus*, servals *Caracal serval* and black-footed cats *Felis nigripes* appear to have evolved

or retained spotted patterns despite a strong preference for open habitats. Furthermore, their sister taxa are generally plain and prefer more closed environments. There are also a number of cats who have plain coats despite preferences for closed environments, more extreme examples being the bay cat *Pardofelis badia* and flat-headed cat *Prionailurus planiceps*. The habitats and behaviour of these cats would have to be compared with closely related, classically camouflaged species in greater detail to understand these apparent deviations from the norm. Plain and patterned cats could be using different microhabitats within the rather broad categories defined in this study. Plain and patterned solutions may have a different camouflage function (e.g. background matching versus disruptive camouflage [47]). Alternatively, plain and patterned camouflage solutions may be similarly effective in some instances or have costs unrelated to camouflage so that no selection pressure away from a particular phenotype is exerted. Some species may simply retain sub-optimal solutions because of a genetic or developmental constraint, although given the evidence that felid patterning is highly labile this seems unlikely. Finally, a recent habitat or pattern shift could account for mismatches: previously effective camouflage patterns can become conspicuous and distinctive recognition cues, while unfamiliar phenotypes may benefit from poorer predator and prey recognition [48]. However, without independent palaeontological evidence, this should be dismissed as an *ad hoc* argument.

Overall the classification method we developed has captured the essence of the visual appearance of cats' patterning very well (figure 2). The main problems with the classifications stem from the limited availability of high-quality images. The background literature suggests our image corpus has captured intricate aspects of pattern variation within and between species successfully—for example, the levels of pattern variation within the lynx lineage, with Canadian lynx *Lynx canadensis* being least patterned and Iberian lynx *Lynx pardinus* most highly patterned [31]. However, the low levels of patterning in lynx and Canadian lynx may be accounted for by patterning being less visible in winter owing to overgrowth by winter pelage (snow cover could be seen in two of the photos of lynx and three of Canadian lynx, but none of Iberian lynx). Other samples may be less representative of the population, although the only example of a clearly unrepresentative sample we could identify was the Asian golden cat *Pardofelis temminckii*, which is known to often be patterned in the north of its range [31]; its classification as plain reflects bias created by the image selection method. However, classified as plain, it opposes the overall trends reported and so does not affect the reliability of the significant findings obtained. Wildcats *Felis silvestris* and Andean mountain cats *Leopardus jacobita* often have indistinct markings that were present in some of the standard images, but evidently observers generally considered these too low a contrast to be meaningful patterns; this may not be the case for other organisms' vision. This effect may also have been involved in classification of some of the other cats that show variation in patterning, such as the lynxes, rusty-spotted cat *Prionailurus rubiginosus*, pampas cat *Leopardus colocolo*, kodkod *Leopardus guigna* and sand cat *Felis margarita*. The classification of wildcats as being plain may also indicate

bias in the image sample away from the European wildcat subspecies *Felis silvestris silvestris*, which anecdotal evidence suggests is generally more strongly patterned than its African (*Felis silvestris lybica* and *Felis silvestris cafra*) and Asian (*Felis silvestris ornata* and *Felis silvestris bieti*) counterparts.

In summary, this study shows that, in general, detailed aspects of felid's flank patterns have evolved to match visual properties of the environments they inhabit and their behaviour within those environments, in order to achieve camouflage supporting the analyses (based on subjective categorical classifications) of Ortolani and Caro [1] and Ortolani [2]. A few species have patterns that general trends do not predict, and these merit further investigation. The major advance reported here is the demonstration that evolved traits (pattern, habitat and behavioural) can be linked to a mathematical model of pattern development. We suggest that future comparative studies of animal coloration should also be linked to specific models of development, as these constrain the variety of pattern expressions as well as affording a parametric basis for analysis. Mathematical models of pattern development have been applied to other taxa with interesting patterning, such as snakes [49] and fish [18], and future studies could go on to link these with ecology. Considerable effort has been directed towards understanding the function and utility of different camouflage patterns in recent years [50]. A challenge for the future, which has begun to be tackled here and elsewhere [1,2,51–53], is to understand when and where particular camouflage solutions and other coloration patterns are employed.

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REFERENCES

- Ortolani, A. & Caro, T. M. 1996 The adaptive significance of color patterns in carnivores: phylogenetic tests of classic hypotheses. In *Carnivore behaviour, ecology and evolution*, vol. 2 (ed. J. Gittleman), pp. 132–188. Ithaca, NY: Cornell University Press.
- Ortolani, A. 1999 Spots, stripes, tail tips and dark eyes: predicting the function of carnivore colour patterns using the comparative method. *Biol. J. Linn. Soc.* **67**, 433–476. (doi:10.1111/j.1095-8312.1999.tb01942.x)
- Caro, T. M. & Fitzgibbon, C. 1992 Large carnivores and their prey: the quick and the dead. In *Natural enemies: the population biology of predators, parasites and diseases* (ed. M. Crawley), pp. 117–142. Oxford, UK: Blackwell Scientific Publications.
- Sunquist, M. E. & Sunquist, F. C. 1989 Ecological constraints in predation by large felids. In *Carnivore behaviour, ecology and evolution*, vol. 1 (ed. J. Gittleman), pp. 283–301. Ithaca, NY: Cornell University Press.
- Elliott, J. P., Cowan, I. M. T. & Holling, C. S. 1977 Prey capture by the African lion. *Can. J. Zool.* **55**, 1811–1828. (doi:10.1139/z77-235)
- Murray, D. 1995 Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. *Anim. Behav.* **50**, 1203–1210. (doi:10.1016/0003-3472(95)80037-9)
- Palomares, F. & Caro, T. M. 1999 Interspecific killing among mammalian carnivores. *Am. Nat.* **153**, 482–508. (doi:10.1086/303189)
- Maddison, D. R. & Maddison, W. P. 1992 *Maclade: analysis of phylogeny and character evolution*. Version 3.04. Sunderland, MA: Sinauer.
- Godfrey, D., Lythgoe, J. N. & Rumball, D. A. 1987 Zebra stripes and tiger stripes: the spatial frequency distribution of the pattern compared to that of the background is significant in display and crypsis. *Biol. J. Linn. Soc.* **32**, 427–433. (doi:10.1111/j.1095-8312.1987.tb00442.x)
- Kiltie, R. A., Fan, J. & Laine, A. F. 1994 A wavelet-based metric for visual texture discrimination with applications in evolutionary ecology. *Math. Biosci.* **126**, 21–39. (doi:10.1016/0025-5564(94)00034-w)
- Stevens, M. & Cuthill, I. C. 2006 Disruptive coloration, crypsis and edge detection in early visual processing. *Proc. R. Soc. B* **273**, 2141–2147. (doi:10.1098/rspb.006.3556)
- Stoddard, M. C. & Stevens, M. 2010 Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proc. R. Soc. B* **277**, 1387–1393. (doi:10.1098/rspb.2009.2018)
- Stevens, M., Párraga, C. A., Cuthill, I. C., Partridge, J. C. & Troscianko, T. S. 2007 Using digital photography to study animal coloration. *Biol. J. Linn. Soc.* **90**, 211–237. (doi:10.1111/j.1095-8312.2007.00725.x)
- Osorio, D., Miklósi, A. & Gonda, Z. 1999 Visual ecology and perception of coloration patterns by domestic chicks. *Evol. Ecol.* **13**, 673–689. (doi:10.1023/A:1011059715610)
- Gibson, B. M., Lazareva, O. F., Schyns, P. G. & Wasserman, E. A. 2007 Nonaccidental properties underlie shape recognition in mammalian and non-mammalian vision. *Curr. Biol.* **17**, 336–340. (doi:10.1016/j.cub.2006.12.025)
- Werdelin, L. & Olsson, L. 1997 How the leopard got its spots: a phylogenetic view of the evolution of felid coat patterns. *Biol. J. Linn. Soc.* **62**, 383–400. (doi:10.1006/bijl.1997.9999)
- Eizirik, E., David, V. A., Buckley-Beason, V., Roelk, M. E., Schäffer, A. A., Hannah, S. S., Narfström, K., O'Brien, S. J. & Menotti-Raymond, M. 2010 Defining and mapping mammalian coat pattern genes: multiple genomic regions implicated in domestic cat stripes and spots. *Genetics* **184**, 267–275. (doi:10.1534/genetics.109.109629)
- Kondo, S. 2002 The reaction diffusion system: a mechanism for autonomous pattern formation in the animal skin. *Genes Cells* **2**, 535–541. (doi:10.1046/j.1365-2443.2002.00543.x)
- Murray, J. D. 2003 *Mathematical biology II: spatial models and biomedical applications*, 3rd edn. New York, NY: Springer-Verlag.
- Turk, G. 1991 Generating textures on arbitrary surfaces using reaction–diffusion. *Comp. Graph.* **25**, 289–298. (doi:10.1145/127719.122749)
- Graván, C. P. & Lahoz-Beltra, R. 2004 Evolving morphogenetic fields in the zebra skin pattern based on Turing's morphogen hypothesis. *Int. J. Appl. Math. Comput. Sci.* **3**, 351–361.
- Bond, A. B. & Kamil, A. C. 2002 Visual predators select for crypticity and polymorphism in virtual prey. *Nature* **415**, 609–613. (doi:10.1038/415609a)
- Bond, A. B. & Kamil, A. C. 2006 Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proc. Natl Acad. Sci. USA* **103**, 3214–3219. (doi:10.1073/pnas.0509963103)
- Tinbergen, N. 1963 On aims and methods in ethology. *Z. Tierpsychol.* **20**, 410–433. (doi:10.1111/j.1439-0310.1963.tb01161.x)

- 25 Galeotti, P., Rubolini, D., Dunn, P. O. & Fasola, M. 2003 Colour polymorphism in birds: causes and functions. *J. Evol. Biol.* **16**, 635–646. (doi:10.1046/j.1420-9101.2003.00569.x)
- 26 Bard, J. & Lauder, I. 1974 How well does Turing's theory of morphogenesis work? *J. Theor. Biol.* **45**, 501–531. (doi:10.1016/0022-5193(74)90128-3)
- 27 Bard, J. 1981 A model for generating aspects of zebra and other mammalian coat patterns. *J. Theor. Biol.* **93**, 363–385. (doi:10.1016/0022-5193(81)90109-0)
- 28 Kitchener, A. 1991 *The natural history of the wild cats*. London, UK: Christopher Helm Publishers.
- 29 Nowack, R. M. 1999 *Walker's mammals of the world*, 6th edn. Baltimore, MD: John Hopkins University Press.
- 30 Macdonald, D. 2001 *The new encyclopedia of mammals*. Oxford, UK: Oxford University Press.
- 31 Sunquist, M. E. & Sunquist, F. C. 2002 *Wild cats of the world*. Chicago, IL: Chicago University Press.
- 32 Meachen-Samuels, J. & Van Valkenburgh, B. 2009 Craniodental indicators of prey size preference in the Felidae. *Biol. J. Linn. Soc.* **96**, 784–799. (doi:10.1111/j.1095-8312.2008.01169.x)
- 33 Robinson, R. 1976 Homologous genetic variation in the Felidae. *Genetica* **46**, 1–31. (doi:10.1007/BF00122514)
- 34 Merilaita, S., Toumi, J. & Jormalainen, V. 1999 Optimization of cryptic coloration in heterogeneous habitats. *Biol. J. Linn. Soc.* **67**, 151–161. (doi:10.1111/j.1095-8312.1999.tb01858.x)
- 35 Grafen, A. 1989 The phylogenetic regression. *Proc. R. Soc. Lond. B* **326**, 119–157. (doi:10.1098/rstb.1989.0106)
- 36 Pagel, M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
- 37 Freckleton, R. P., Harvey, P. H. & Pagel, M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726. (doi:10.1086/343873)
- 38 Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**, 247–251. (doi:10.1093/bioinformatics/11.3.247)
- 39 Paradis, E., Claude, J. & Strimmer, K. 2004 APE: analyses of phylogenetics and evolution in the R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
- 40 R Development Core Team. 2007 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- 41 Johnson, W. E., Eizirik, E., Pecon-Slattery, J., Murphy, W. J., Antunes, A., Teeling, E. & O'Brien, S. J. 2006 The late Miocene radiation of modern Felidae: a genetic assessment. *Science* **311**, 73–77. (doi:10.1126/science.1122277)
- 42 Driscoll, C. A., Menotti-Raymond, M., Roca, A. L., Hupe, K. & Johnson, W. E. 2007 The Near Eastern origin of cat domestication. *Science* **317**, 519–523. (doi:10.1126/science.1139518)
- 43 Werdelin, L., Yamaguchi, N., Johnson, W. E. & O'Brien, S. J. 2010 Felid phylogenetics and evolution. In *The biology and conservation of wild felids* (eds D. M. Macdonald & A. Loveridge), pp. 59–82. Oxford, UK: Oxford University Press.
- 44 Zar, J. H. 1974 *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall.
- 45 Kipling, R. 1902 *Just so stories*. London, UK: Macmillan.
- 46 Endler, J. A. 1993 The color of light in forests and its implications. *Ecol. Mono.* **63**, 1–27. (doi:10.2307/2937121)
- 47 Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, A. & Troscianko, T. S. 2005 Disruptive coloration and background pattern matching. *Nature* **434**, 72–74. (doi:10.1038/nature03312)
- 48 Stankowich, T. & Coss, R. G. 2008 The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. *Proc. R. Soc. B* **274**, 175–182. (doi:10.1098/rspb.2006.3716)
- 49 Murray, J. D. 1991 Pigmentation pattern formation on snakes. *J. Theor. Biol.* **149**, 339–360. (doi:10.1016/S0022-5193(05)80310-8)
- 50 Stevens, M. & Merilaita, S. 2009 Animal camouflage: current issues and new perspectives. *Phil. Trans. R. Soc. B* **364**, 423–427. (doi:10.1098/rstb.2008.0217)
- 51 Gomez, D. & Théry, M. 2007 Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a neotropical rainforest bird community. *Am. Nat.* **169**, S42–S61. (doi:10.1086/510138)
- 52 Caro, T. 2009 Contrasting coloration in terrestrial mammals. *Phil. Trans. R. Soc. B* **364**, 537–548. (doi:10.1098/rstb.2008.0221)
- 53 Kamilar, J. M. 2009 Interspecific variation in primate countershading: effects of activity pattern, body mass, and phylogeny. *Int. J. Primatol.* **30**, 877–891. (doi:10.1007/s10764-009-9359-9)