

# 1 Fluffy feathers: how neoptile feathers contribute to 2 camouflage in precocial chicks

3 Running title: Chick feathers improve outline diffusion

4 **Authors:** Veronika A. Rohr<sup>1,2</sup>, Tamara Volkmer<sup>3</sup>, Dirk Metzler<sup>2</sup>, Clemens Küpper<sup>1</sup>

5 <sup>1</sup> Research Group for Behavioural Genetics and Evolutionary Ecology, Max Planck Institute for  
6 Ornithology, Seewiesen, Germany

7 <sup>2</sup> Division of Evolutionary Biology, Faculty of Biology, Ludwig-Maximilians-Universität München,  
8 Planegg-Martinsried, Germany

9 <sup>3</sup> Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany

10 **Mail:** vrohr@orn.mpg.de; ckuepper@orn.mpg.de

## 11 Keywords

12 Irregular marginal form, camouflage, skin filaments, feathers, edge intensity, contour perception

## 13 Abstract

14 Camouflage is a widespread strategy to increase survival. The plumage of precocial chicks often  
15 contains elements of disruptive colouration and background matching to enhance concealment. Chick  
16 plumage also features fringed feathers as appendages that may contribute to camouflage. Here, we  
17 examine whether and how neoptile feathers conceal the outline of chicks. We first conducted a digital  
18 experiment to test two potential mechanisms for outline diffusion through appendages: 1) edge  
19 intensity reduction and 2) luminance transition. Local Edge Intensity Analysis (LEIA) showed that  
20 appendages decreased edge intensity and a mean luminance comparison revealed that the  
21 appendages created an intermediate transition zone to conceal the object's outline. The outline was  
22 most diffused through an intermediate number of interspersed thin appendages. Increased appendage  
23 thickness resulted in fewer appendages improving camouflage, whereas increased transparency  
24 required more appendages for best concealment. For edge intensity, the outline diffusion was  
25 strongest for a vision system with low spatial acuity, which is characteristic of many mammalian  
26 predators. We then analysed photographs of young snowy plover (*Charadrius nivosus*) chicks to  
27 examine whether neoptile feathers increase outline concealment in a natural setting. Consistent with  
28 better camouflage, the outline of digitally cropped chicks with protruding feathers showed lower edge  
29 intensities than the outline of chicks cropped without those feathers. However, the observed mean  
30 luminance changes were not consistent with better concealment. Taken together, our results suggest

31 that thin skin appendages such as neoptile feathers improve camouflage. As skin appendages are  
32 widespread, this mechanism may apply to a large variety of organisms.

## 33 Introduction

34 Avoiding detection either for protection from predators or to go unnoticed by potential prey is  
35 essential for individual survival. The threat of predation has led to the evolution of various camouflage  
36 mechanisms, which make potential prey more difficult to detect or recognize. The most prominent  
37 mechanism is visual camouflage that includes highly adaptive colouration strategies among animals  
38 (Stevens and Merilaita 2009). One strategy to achieve visual camouflage is background matching (also  
39 termed “crypsis” by Endler (1981)). For background matching, animals try to match colour, luminance  
40 and pattern of their background.

41 While background matching is one of the most common and frequently studied strategies of visual  
42 camouflage (Cott 1940, Endler 1981, Farkas et al. 2013, Allen et al. 2015, Stevens et al. 2017), another  
43 important mechanism is concealing the outline of the body. Thayer (1909) proposed that detecting the  
44 outline of their prey is one of the ways predators locate and identify their prey. In general, the  
45 detection of edges is an essential task for object recognition (Marr 1976, Tovée 1996). In this regard,  
46 disruptive colouration makes animals less detectable. It involves a set of markings that creates false  
47 edges within the animal hindering the detection or recognition of its true outline and shape or parts  
48 of it (Thayer 1909, Cott 1940, Stevens and Merilaita 2009). Cott (1940) suggested that structural  
49 modifications of the organism’s outline themselves could contribute to camouflage by creating an  
50 ‘irregular marginal form’. This makes the animal’s true body outline effectively diffused and hence  
51 makes it harder to detect (Cott 1940). Recently, support for the ‘irregular form’ hypothesis was found  
52 in an experimental study showing that false holes markings reduce avian predations (Costello et al.  
53 2020).

54 Birds with their typically advanced vision and high plumage diversity have been featured prominently  
55 in camouflage research, either as predators or as prey (Cuthill et al. 2005, Skelhorn et al. 2010, Farkas  
56 et al. 2013, Lovell et al. 2013, Stevens et al. 2017, Pike 2018, Costello et al. 2020). When studying  
57 camouflage as an anti-predator defence in birds, much research has examined the clutches/eggs of  
58 ground-nesting birds (Stoddard et al. 2011, Ekanayake et al. 2015, Stevens et al. 2017). These studies  
59 revealed that ground-nesting birds may increase background matching through adaptive egg  
60 colouration that matches the nest site (Lovell et al. 2013, Stevens et al. 2017) and some species even  
61 improve the background matching of their clutches, by soiling their eggs to conceal them better  
62 (Mayani-Parás et al. 2015), using egg-matching nest materials (Gómez et al. 2018) or covering the  
63 clutch with debris or soil when predators approach (Troscianko et al. 2016).

64 However, not only eggs are vulnerable to predation. Chicks are also often targeted by predators.  
65 Precocial chicks leave their nest within a few hours of hatching. Initially, those chicks suffer from high  
66 mortality as they are limited in their mobility and hence highly vulnerable to predation (Colwell et al.  
67 2007, Brudney et al. 2013, Eberhart-Phillips et al. 2018). To improve their survival, chicks rely on  
68 camouflage provided by their feathers especially during the first days of their lives. The plumage  
69 colouration of precocial chicks featured prominently in the description of camouflage mechanisms  
70 such as disruptive colouration (Thayer 1909, Cott 1940, Hill and McGraw 2006). However, we know  
71 surprisingly little about plumage characteristics that improve camouflage in chicks. Precocial chicks  
72 hatch fully covered with neoptile down feathers (Foth 2011). With maturation, the neoptile feathers  
73 are shed, and the natal plumage is replaced by the teleoptile feathers, which can be categorised into,  
74 e.g. flight, contour and down feathers (Stettenheim 1976). One striking feature of neoptile feathers is  
75 that they are protruding from the chick's body. The unequal length of the very thin feathers creates a  
76 fringed feather region that may conceal the chick outline and hence make it harder to detect by  
77 predators.

78 In this study, we investigated whether neoptile down feathers improve camouflage through outline  
79 diffusion. Cott (1940) discussed this strategy of an 'irregular marginal form' mainly with examples of  
80 masquerade, where the irregular shapes of animals resemble elements of their environment, e.g. parts  
81 of plants. In contrast, we hypothesized that the fringed feathery outline helps the chick to better blend  
82 with the background by reducing edge contrasts and/or creating a transition zone of intermediate  
83 luminance.

84 In a first experiment, we explored the mechanism of outline diffusion by appendages in principle  
85 modelling a circular object with varying protruding appendages. We then used the Local Edge Intensity  
86 Analysis (LEIA) (van den Berg et al. 2019) to investigate whether appendages decreased the edge  
87 contrast of the object's outline. Additionally, we investigated how appendage characteristics such as  
88 their density, thickness, transparency, and variation in background complexity and spatial acuity of the  
89 predator's visual system affected edge intensity in the contour region. As a second mechanism, we  
90 tested whether appendages altered the luminance of a narrow 'transition zone' between object and  
91 background. We hypothesized that an intermediate mean luminance in the transition zone that  
92 reduces the contrast would help to blend the object better with the background.

93 In a second experiment, we tested whether the neoptile feathers contribute to the camouflage of  
94 precocial chicks. We analysed images taken from precocial snowy plover (*Charadrius nivosus*) chicks in  
95 natural habitats. Very young plover chicks rely on their crypsis to evade predation as they stay  
96 motionless on the ground when a threat is approaching (Colwell et al. 2007). We digitally cropped all  
97 chicks once with and once without protruding feathers and transferred them on to images of their

98 hiding background taken after gently removing the chicks. For chicks cropped with their protruding  
99 feathers, we predicted the edge intensity of the chick outline to be reduced and the mean luminance  
100 difference of the transitions zone to be closer to intermediate optimum than for the images of those  
101 chicks cropped without their feathers.

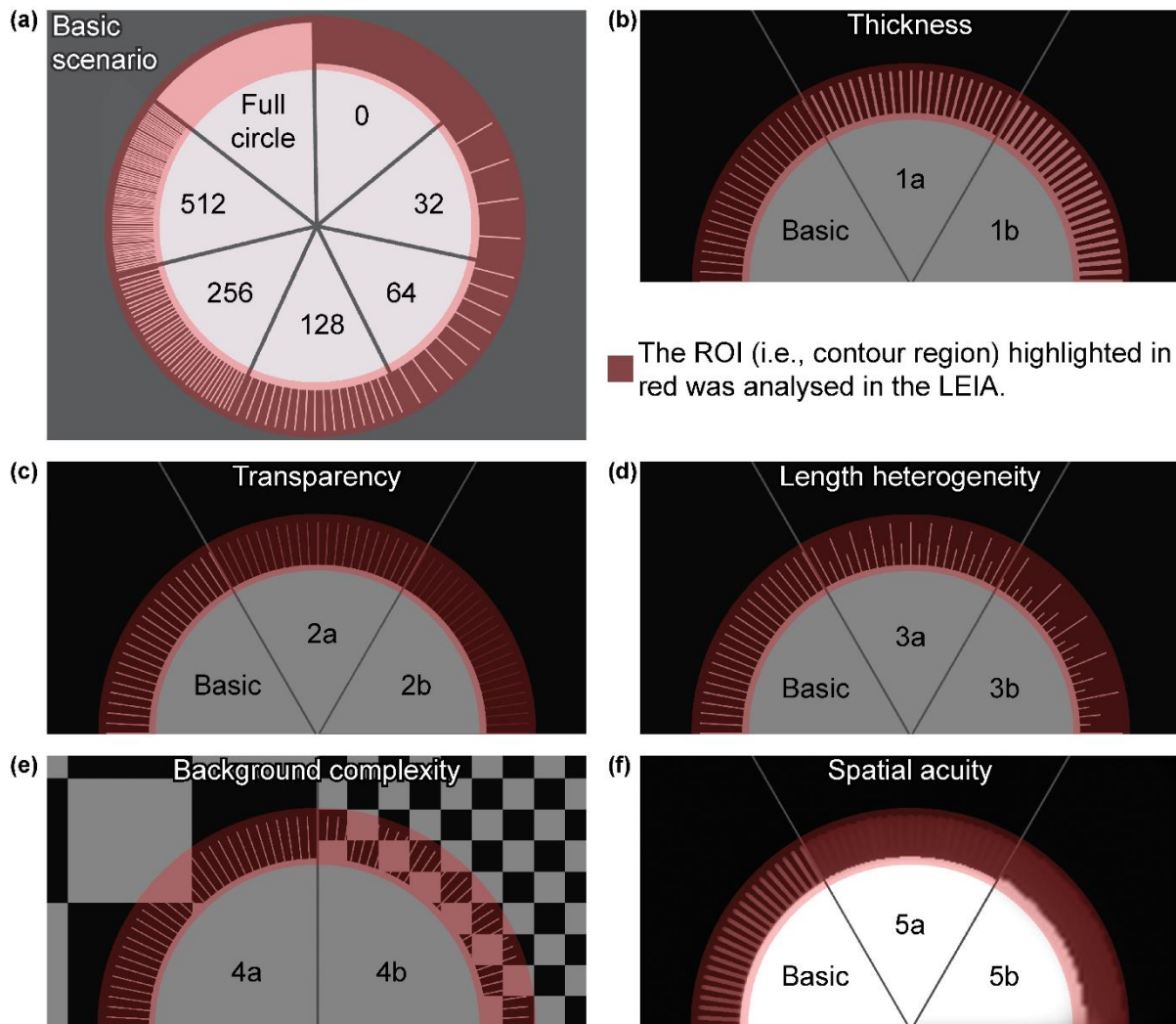
## 102 Material and methods

### 103 Experiment 1: Proof of principle

104 As a proof of principle, we designed the first experiment to test whether appendages may help to  
105 conceal the outline. We created an image of a uniformly light grey coloured circular object with a size  
106 of 2950 pixels (px)/250.0 mm circumference and 470 px/39.8 mm radius on a dark grey background.  
107 The initial setup started with no appendages added to the outline (Figure 1a, '0'). We then added  
108 object-coloured appendages (i.e. lines of 1 Pt/4 px/0.4 mm thickness and 118 px/10.0 mm length) with  
109 regular intervals resembling protruding neoptile chick feathers orthogonally to the object outline  
110 ('Basic Scenario', Figure 1a). The first image with appendages had 32 appendages added to the outline  
111 (Figure 1a, '32'). We then doubled the number of appendages stepwise creating denser spaced  
112 appendages to the outline until the extended outline was completely filled (Figure 1a, 'full circle'). For  
113 the vision of a simulated predator, we used the spatial acuity from humans (*Homo sapiens*, 72 cycles  
114 per degree, cpd) (Land 1981; Land and Nilsson 2012; Caves and Johnsen 2018) in the basic scenario.  
115 The full details for the parameters are provided in Table S1 (a to g).

116 To further explore the mechanism, we altered appendage characteristics, background and the spatial  
117 acuity of the predator. First, we increased appendage thickness to 2 Pt/8 pixels/ 0.7 mm (Scenario 1a)  
118 and 3 Pt/12 pixels/1.1 mm (Scenario 1b) resulting in decreased inter-appendage intervals (Figure 1b  
119 and Table S1, h to u). Second, we changed appendage transparency to 25 % (Scenario 2a) and 50 %  
120 transparency (Scenario 2b) (Figure 1c and Table S1, v to ai). Third, we varied the appendage length  
121 heterogeneity; half of the appendages having 50 % of the length (Scenario 3a), and half of the  
122 appendages at 25 % and one quarter at 50 % of the original appendage length (Scenario 3b) (Figure 1d  
123 and Table S1, aj to aw). Fourth, we investigated the effect of background complexity on the  
124 detectability of the outline. As background, we used a chessboard pattern with large squares  
125 (346 pixels/29.3 mm, Scenario 4a) and with small squares (86 pixels/7.3 mm, Scenario 4b) (Figure 1e  
126 and Table S1, ax to bk). Fifth, we altered the spatial acuity to test whether or how the visual systems  
127 of different predators would affect detectability. We simulated the spatial acuity of a corvid predator  
128 (30 cpd, Scenario 5a) and canid predator (10 cpd, Scenario 5b) (Figure 1f and Table S1, bl to by), the  
129 two most common predators of ground-nesting plovers (Burrell and Colwell 2012, Ekanayake et al.  
130 2015, Ellis et al. 2020). This range also covered other potential predators (Table S2).

131 We did not account for differences in colour vision between different predators as the setup mostly  
132 consists of greyscale images that predominantly differ in luminance. Note that in many animals, visual  
133 acuity is greater for achromatic than chromatic stimuli (Giurfa et al. 1997, Endler et al. 2018).



134  
135 **Figure 1:** (a) Basic Scenario: Seven stages of the artificial chick setup with varying number of thin, non-transparent appendages  
136 having all the same length. (b) Scenario 1: varying appendage thickness applied to the Basic Scenario. (c) Scenario 2: varying  
137 appendage transparency applied to the Basic Scenario. (d) Scenario 3: varying appendage length heterogeneity applied to the  
138 Basic Scenario. (e) Scenario 4: varying background complexity with artificial chessboard backgrounds. (f) Scenario 5: high,  
139 medium and low visual acuity applied to the Basic Scenario. (a – f) The analysed region of interest (ROI) is highlighted in red  
140 for clarification only.

141 We conducted visual modelling and visual analysis using the Quantitative Colour Pattern Analysis  
142 (QCPA) framework (van den Berg et al. 2019) integrated into the Multispectral Image Analysis and  
143 Calibration (MICA) toolbox (Troscianko and Stevens 2015) for ImageJ version 1.52a (Schneider et al.  
144 2012). We converted the generated images into multispectral images containing the red, green and  
145 blue channel in a stack and transformed them further into 32-bits/channel cone-catch images based  
146 on the human visual system, which are required by the framework. To create the luminance channel,

147 we averaged the long and medium wave channel, which is thought to be representative of human  
148 vision (Livingstone and Hubel 1988) (Figure S1a). We modelled the spatial acuity with Gaussian Acuity  
149 Control at a viewing distance of 1300 mm and a minimum resolvable angle (MRA) of 0.01389 (Figure  
150 S1b). To increase biological accuracy, we applied a Receptor Noise Limited (RNL) filter that reduces  
151 noise and reconstructs edges in the image. The RNL filter used the Weber fractions “Human 0.05”  
152 provided by the framework (longwave 0.05, mediumwave 0.07071, shortwave 0.1657), luminance 0.1,  
153 5 iterations, a radius of 5 pixels and a falloff of 3 pixels (Figure S1c) as specified in van den Berg et al.  
154 (2019).

#### 155 Local Edge Intensity Analysis

156 To test for the detectability of the outline, we used LEIA (van den Berg et al. 2019), which is  
157 conceptually similar to the boundary strength analysis (Endler et al. 2018). Boundary strength analysis  
158 requires an image with clearly delineated (clustered) colour and luminance pattern elements.  
159 However, a large degree of subthreshold details, which may be still perceived by the viewer gets lost  
160 in the clustering process. LEIA has the advantage of not requiring such a clustered input and therefore  
161 can be directly applied to RNL filtered images. LEIA measures the edge intensity (i.e. the luminance  
162 contrast) locally at each position in the image. The output image displays  $\Delta S$  values in a 32-bit stack of  
163 four slices, where each slice shows the values measured in different angles (horizontal, vertical and  
164 the two diagonals, for more details, see van den Berg et al. (2019)).

165 We ran LEIA on the chosen region of interest (ROI) with the same Weber fractions used for the RNL  
166 filter. The ROI was the contour region, a 180 pixel-wide band that included the area of the appendages  
167 extended by 30 pixels towards the object inside and towards the outside (Figure 1a). We log-  
168 transformed the  $\Delta S$  values as recommended for natural scenes (Troscianko and van den Berg 2020) to  
169 make the results comparable to the natural background images used in Experiment 2 (see below). To  
170 test whether the size of the ROI affected our results, we ran an additional analysis using a 1500 x 1500  
171 pixel-wide rectangle surrounding the object as the ROI, which included a bigger area of the background  
172 and the full object inside (Figure S2a).

173 We extracted the luminance  $\Delta S$  values from the four slices of the output image stack in ImageJ and  
174 stored them in separate matrices for further analysis using R version 3.5.3 (R Core Team 2019). ImageJ  
175 generally assigned values outside the chosen ROI to zero. Thus, we first discarded all values of zero.  
176 We then set all negative values that arose as artefacts in areas without any edges to zero, in order to  
177 make them biologically meaningful. We then identified the parallel maximum (R function  $pmax()$ ) of  
178 the four interrelated direction matrices and transferred this value to a new matrix.



179 High luminance and colour contrasts imply high conspicuousness (Endler et al. 2018). Consequently, a  
180 lower luminance contrast leads to lower conspicuousness and therefore, better camouflage. As the  
181 outline is an important cue for predators locating and identifying a prey item (Thayer 1909), we  
182 assumed that especially low contrasts in the outline of an object improve camouflage. Thus, a  
183 reduction of edge intensity in the object outline by the appendages indicates a camouflage  
184 improvement. To test whether the object outline became less detectable we compared the edge  
185 intensity of the outline pixels in the basic scenario without appendages (Table S1, a) with  
186 corresponding pixels from other scenarios. The outline pixels were characterised by high edge intensity  
187 and constituted a prominent peak. They comprised 1.59 % of all pixels in the analysis focused on the  
188 contour region (see Results, Figure 2a). For all scenarios, we calculated the mean edge intensity of the  
189 high edge intensity pixels (HEI pixels) and identified the changes with parameter variation.

#### 190 Mean Luminance Comparison

191 For the Mean Luminance Comparison (MLC), we analysed the same images as with the LEIA. We  
192 divided the filtered image into three regions of interest (ROIs) (Figure 3a). 1) The object region included  
193 the whole object inside up to 20 pixels next to the object outline. 2) The appendage region was an  
194 80 pixel-wide band including only the area covered by appendages. It started 20 pixels outside the  
195 object outline and reached up to 20 pixels before the boundary created by the appendages  
196 (appendage-boundary). 3) The background region ranged from 20 pixels outside the appendage-  
197 boundary to a 1500x1500 pixel-wide rectangle surrounding the object. A buffer zone of 40 pixels  
198 between all three regions was excluded from the analysis to ensure a clear separation of the regions.  
199 In the luminance channel of each image, we measured the mean luminance in the three regions and  
200 compared them subsequently. Luminance values range from 0 to 1.

201 According to background matching, objects that differ more in luminance from the background are  
202 more conspicuous and hence less well camouflaged (Endler 1981). We assumed that detectability  
203 based on possible luminance differences between object and background are weakened by the  
204 appendages as they form a transition zone helping to blend the object better into the background.  
205 Accordingly, from a camouflage perspective, the appendage region would provide an optimal  
206 transition zone when its mean luminance is exactly the mean of the object and background region's  
207 luminance.

#### 208 Experiment 2: Chick photographs

209 Using pictures of young snowy plover chicks hiding when approached by a predator, we tested if  
210 protruding neoptile feathers helped to conceal the chicks' outline and therefore improve their  
211 camouflage.

212 We studied snowy plovers in their natural environment at Bahía de Ceuta, Sinaloa, Mexico. The  
213 breeding site consists of salt flats that are sparsely vegetated and surrounded by mangroves (Cruz-  
214 López et al. 2017). General field methodology is provided elsewhere (Eberhart-Phillips et al. 2020). In  
215 2017, we took photographs of young (one to three days old) chicks hiding on the ground, that had  
216 already left the nest scrape. To photograph the chicks, two observers approached free-roaming  
217 families with two mobile hides (Székely et al. 2008) within the period one hour after sunrise and one  
218 hour before sunset. At a distance of 100-200 m, one observer acted as ‘predator’, left the hide and  
219 openly approached the brood while the second observer kept watching the chicks. The chicks  
220 responded by crouching to the ground and staying motionless while the parents were alarming. The  
221 second observer directed the ‘predator’ to the approximate hiding place. When searching for the  
222 chicks, we took great care to reduce the number of steps to avoid modification of the ground through  
223 our tracks.

224 Once the first chick had been found, the second observer joined the predator and took chick  
225 photographs. We used a Nikon D7000 camera converted to full spectrum including the UV range (Optic  
226 Makario GmbH, Germany) and a Nikkor macro 105 mm lens that allows transmission of light at low  
227 wavebands. The equipment was chosen because calibration data were available for this combination  
228 (Troscianko and Stevens 2015). Each hiding background was photographed with and without the chick  
229 using a UV pass filter for the UV spectrum and a UV/IR blocking filter (“IR – Neutralisationsfilter NG”,  
230 Optic Makario GmbH, Germany) for the visible spectrum. The camera was set to an aperture of f/8,  
231 ISO 400 and the pictures were stored in “RAW” file format. We used exposure bracketing to produce  
232 three images to ensure that at least one picture was not over or underexposed. A 25 % reflectance  
233 standard (Zenith Polymer TM) placed in the corner of each picture enabled a subsequent standardizing  
234 of light conditions.

235 In total, we took pictures of 32 chicks from 15 families. For 21 chicks we obtained photographs suitable  
236 for further analyses with an unobstructed view to the entire chick and only one chick per photograph.  
237 Of these, we randomly selected pictures of 15 chicks. Unfortunately, it was not possible to obtain  
238 proper alignment of visual and UV pictures in ImageJ as either chick or camera moved slightly in the  
239 break between changing filters for the two settings. Therefore, we restricted our analyses to human  
240 colour vision and discarded the UV pictures for further analysis.

241 In each picture, we manually selected the chick outline and the feather-boundary as a basis for the  
242 ROIs (Figure 4a-c). The chick outline included bill, legs, rings and all areas densely covered by feathers  
243 without background shining through. We then marked the feather-boundary, i.e., the smoothed line  
244 created by the protruding neoptile feather tips. In the next step, we transferred images of chicks with  
245 or without protruding feathers, i.e. cropped at feather-boundary or chick outline, respectively, and



246 inserted them into a uniform or the natural background. First, we cropped the chick without protruding  
247 feathers and transferred it into a uniform black background. Second, we cropped the chick including  
248 all feathers and inserted it into exactly the same hiding spot on the picture of the natural background  
249 (Figure 4b). Third, we cropped the chick excluding the protruding feathers and transferred it into the  
250 natural background (Figure 4c).

#### 251 Local Edge Intensity Analysis

252 We then proceeded with LEIA following the protocol of experiment 1 with the following changes.  
253 Again, the selected ROI was the contour region ranging from the chick outline extended by 30 pixels  
254 towards the chick inside to the feather-boundary extended by 30 pixels towards the outside. We  
255 excluded all areas of the ROI that showed a shadow of the chick as the chicks' shadow was missing on  
256 the empty natural background images to which the cropped chicks were transferred to (Figure 4a-c).  
257 We used the images of the cropped chicks on the black background to determine the threshold of the  
258 HEI pixels according to the protocol of experiment 1 for each chick separately. For each cropped chick  
259 that was transferred to the picture with the natural background, we compared the mean edge intensity  
260 of the HEI pixels provided by LEIA with and without protruding feathers (Figure 4b-c) using a two-sided  
261 paired t-test.

#### 262 Mean Luminance Comparison

263 We also calculated mean luminance differences for each chick using the same cropped photographs  
264 as for the LEIA. Similar to the artificial object experiment, the chick region included everything inside  
265 the chick outline, the background region included everything outside the feather-boundary up to a  
266 1500x1500 pixel-wide rectangle surrounding the chick and the feather region (FR) was between chick  
267 outline and feather-boundary. Note that the FR is different from the contour region, which additionally  
268 includes a small part of chick and background region. We reduced the FR by excluding all areas that  
269 were shaded by the chick since this shadow was missing on the empty background images.  
270 Additionally, we excluded the buffer zone (Figure 3a, the area between the coloured regions) to cover  
271 the whole variation in feather density in the FR (Figure 5a-b). Close to the chick outline, the feathers  
272 were still relatively dense thinning more and more towards the feather-boundary as they were very  
273 variable in length.

274 For each chick, we measured the mean luminance of all three regions in the luminance channel of the  
275 image containing the chick without feathers (Figure 5a). The FR we measured again in the image  
276 containing the chick with feathers (Figure 5b).

277 In theory, the best transition zone between chick and background that reduces the outline of the chick  
278 against the background the most should have an exactly intermediate luminance between chick and

279 background region. In a first analysis, we checked whether the absolute distance of mean luminance  
280 of the FR with feathers was closer to those optimal values than without feathers. Because the  
281 luminance data were not normally distributed according to the Shapiro-Wilk normality test we  
282 conducted a Wilcoxon paired signed rank test. To compare the data graphically in an intuitive way, we  
283 transformed the values so that the chick region always was the reference with a value of 0, the  
284 background region became 1. The two values measured in the FR stayed in their initial relative distance  
285 to chick and background value.

286 The FR generally was quite narrow compared to chick and background region and its effect probably  
287 acts predominantly from close proximity. Therefore, we focussed the next analysis only on chick and  
288 FR. We assumed that the chick to a certain extent differs in luminance from its immediate background  
289 in the FR and that including the feathers decreases this difference and thus possibly improves the  
290 camouflage. Therefore, we compared the absolute distances between the mean luminance of chick  
291 region and FR with and without feathers. As the data were normally distributed according to the  
292 Shapiro-Wilk normality test we conducted a two-sided paired t-test.

293 For an easier comparison of the measurements, we transformed the luminance values in this analysis.  
294 The chick region again was the reference with a value of 0. As the background region was excluded,  
295 we scaled the FR without feathers to 1. The value measured in the FR with feathers stayed in its initial  
296 relative distance to the other two values.

297 The analysis aimed to check if the FR meets the basic requirement of a transition zone having  
298 intermediate luminance. Thus, we checked whether the mean luminance value of the FR with feathers  
299 fell between the one of chick region (mean luminance = 0) and FR without feathers (mean  
300 luminance = 1) constituting the immediate surrounding background to account for the local scale. We  
301 calculated the probability for the FR with feathers of having a value between 0 and 1 when randomly  
302 distributed. For this, we drew a random sample ( $n = 10,000$ ) from a normal distribution with the mean  
303 and standard deviation in the transformed data. Then, we ran an exact binomial test to determine  
304 whether the observed intermediate luminance value was different from the expected value.

## 305 Results

### 306 Experiment 1: Artificial object

#### 307 Local Edge Intensity Analysis

308 All images showed multimodal density distributions of pixels (Figure 2a). Pixels showing the highest  
309 edge intensities were found at the object outline. These HEI pixels showed prominent modal peaks in  
310 all multimodal density distributions (Figure 2a). For the object without appendages, 1.59% of pixels

311 made up the distinct modal area with a mean edge intensity of 2.7 (Figure 2a, '0'). Consequently, we  
312 used a threshold of 1.59% to define HEI pixels for all images. Adding appendages reduced the mean  
313 edge intensities of the HEI pixels with the lowest mean edge intensity reached in the image with 256  
314 appendages (Figure 2a-b).

#### 315 *Appendage characteristics*

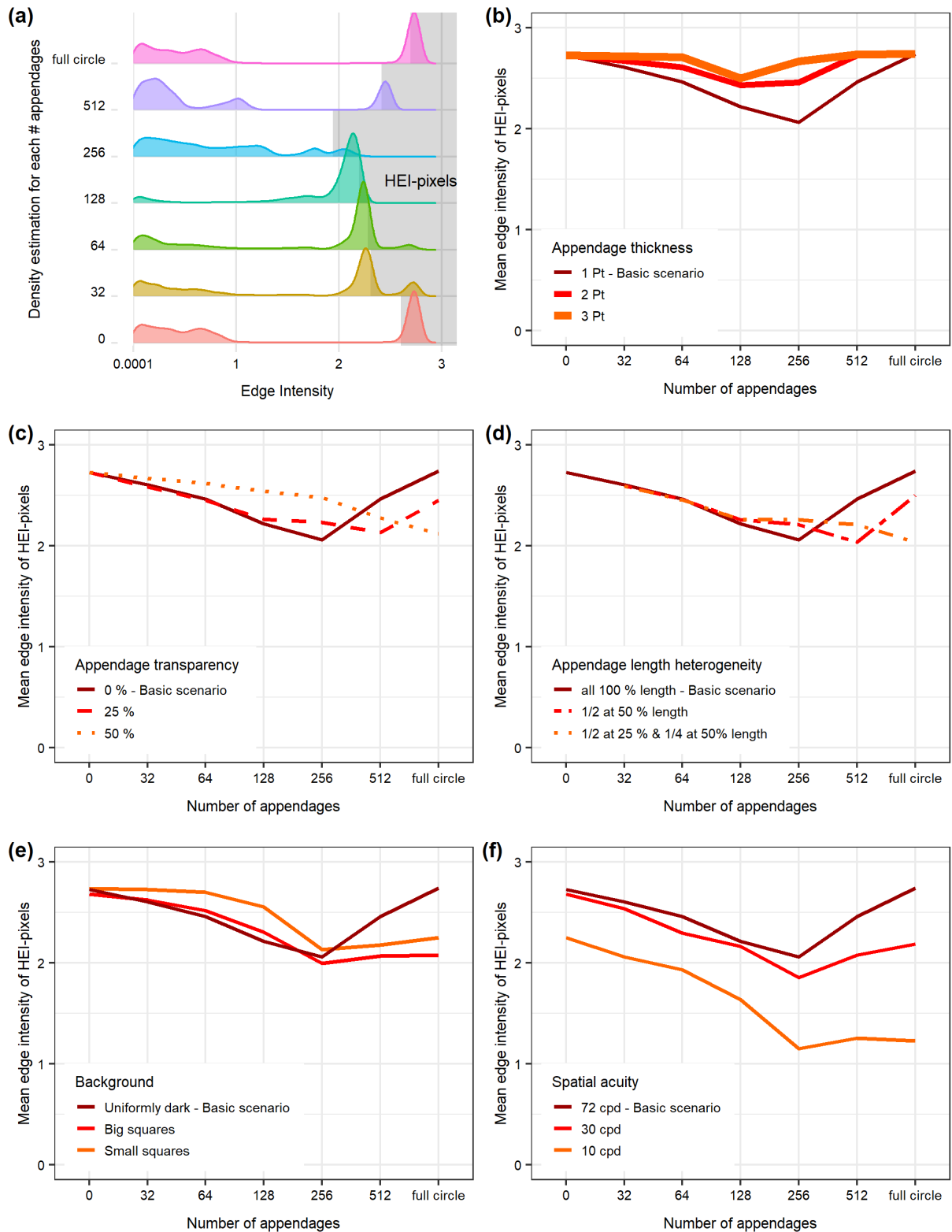
316 Increasing appendage thickness (Scenario 1) resulted in overall higher mean edge intensities  
317 suggesting higher detectability than in the basic scenario. With thicker appendages, the lowest mean  
318 edge intensity of the HEI pixels was reached already with 128 appendages. Images with more than 128  
319 appendages had higher mean edge intensity values implying a deterioration of camouflage (Figure 2b).  
320 Increasing appendage transparency (Scenario 2) yielded overall slightly higher mean edge intensities  
321 than observed in the basic scenario. The lowest mean edge intensities were reached with more  
322 appendages than in the basic scenario (Figure 2c) with the minimum mean edge intensity shown for  
323 512 appendages at 25 % transparency and the full circle of appendages at 50 % transparency (Figure  
324 2c). Increasing appendage length heterogeneity (Scenario 3) yielded the same low mean edge intensity  
325 values as the basic scenario (Figure 2d). However, more appendages were required to reach minimal  
326 mean edge intensity values than in the basic scenario. The minimum mean edge intensity was reached  
327 with 512 appendages when half of the appendages had 50 % of the length or with the full circle when  
328 half of the appendages had 25 % and a quarter had 50 % of the length (Figure 2d).

#### 329 *Background complexity and spatial acuity*

330 Introducing background complexity (Scenario 4) resulted in similar mean edge intensities of the HEI  
331 pixels for 256 appendages as in the basic scenario for large squares. The ROI on the background with  
332 small squares showed slightly higher mean edge intensities for the HEI pixels than for the background  
333 with large squares. More appendages did not lead to such a pronounced increase of mean edge  
334 intensities as in the basic scenario (Figure 2e). Lowering the spatial acuity of the perceiver (Scenario 5)  
335 decreased the mean edge intensity severely. At a spatial acuity of 10 cpd, the minimum mean edge  
336 intensity of the HEI pixels in the image with 256 appendages was only half of the value obtained in the  
337 basic scenario (Figure 2f).

#### 338 *ROI Size*

339 Changing the ROI size and examining a larger part of background and object (Figure S2a) produced  
340 qualitatively similar results (Figure S2b-d, f) except for variation in background complexity (Scenario  
341 4). In that scenario, the number of appendages had no influence on the mean edge intensity of the HEI  
342 pixels (Figure S2e) for the enlarged ROI.



343  
 344 **Figure 2:** Local edge intensity analysis of the contour region in the artificial object experiment. (a) Ridgeline plots showing the  
 345 density distribution of the edge intensity according to number of appendages. The highest 1.59% of the pixels are shaded in  
 346 grey (High edge intensity pixels, HEI pixels). (b) Scenario 1: variation in appendage thickness. (c) Scenario 2: variation in  
 347 appendage transparency. (d) Scenario 3: variation in appendage length. (e) Scenario 4: variation in background complexity.  
 348 (f) Scenario 5: variation in spatial acuity.

### 349 Mean Luminance Comparison

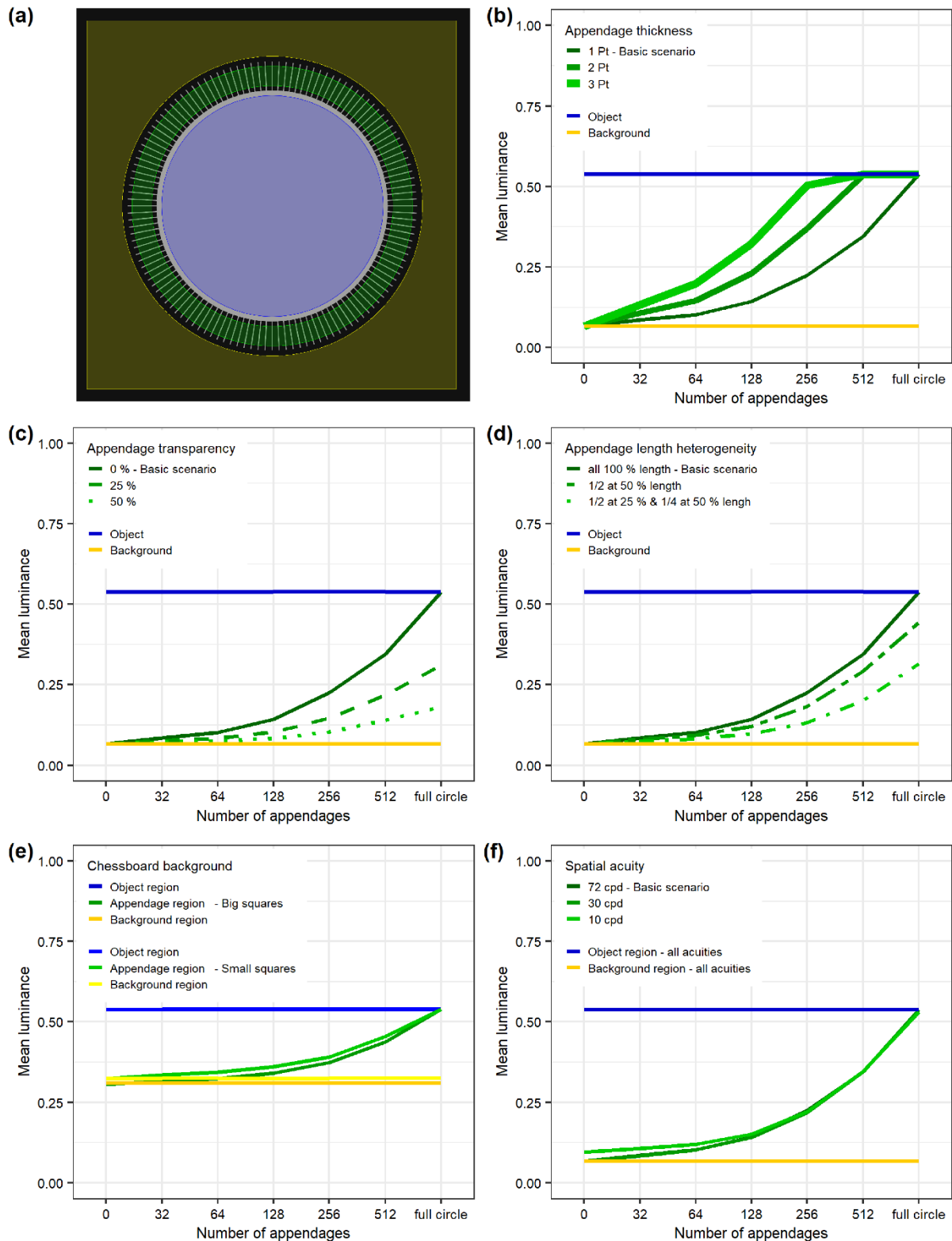
350 The mean luminance of the area covered by appendages (appendage region) was generally  
351 intermediate between the luminance of object and background across all scenarios indicating the  
352 formation of a luminance transition zone (Figure 3b-f). Without appendages, the appendage region's  
353 mean luminance was the same as the one of the background region. With an increasing number of  
354 appendages, the appendage region's mean luminance became more and more similar to the object  
355 region's luminance until they were identical when the appendages formed a full circle (Figure 3b, dark  
356 green curve).

### 357 *Appendage characteristics*

358 Increasing the appendage thickness in Scenario 1 caused the appendage region's luminance to  
359 converge sooner with the object region's luminance. The optimum was also reached sooner, between  
360 128 and 256 appendages at 2 Pt thickness and around 128 appendages at 3 Pt thickness respectively  
361 (Figure 3b). Having 128 appendages of 3 Pt thickness was the best parameter combination tested. In  
362 this image, approximately 50 % of the appendage region's area was covered with appendages. This  
363 suggests for the basic scenario that the optimal intermediate luminance would have been reached for  
364 objects that have between 256 and 512 appendages (Figure 3b, '1Pt'), when 50 % of the appendage  
365 region would have been covered by appendages. In contrast, with increasing appendage transparency  
366 (Scenario 2) more appendages were needed to reach the same luminance values compared to the  
367 Basic Scenario. At 25 % transparency, the full circle of appendages was needed to reach the optimum  
368 intermediate value and with 50% transparency, the intermediate value could not be reached at all  
369 (Figure 3c). Similarly, with increasing appendage length heterogeneity (Scenario 3) more appendages  
370 were required to reach the optimum but it was obtained when half of the appendages had 50 % of the  
371 length as well as when half of the appendages had 25 % and a quarter had 50 % of the length (Figure  
372 3d).

### 373 *Background complexity and spatial acuity*

374 Increasing the background complexity did not affect the curve trajectories in the transition zone.  
375 Without appendages, the appendage region's mean luminance was similar to the background's  
376 luminance and became increasingly similar to the object's luminance when raising the number of  
377 appendages until they converged with a full circle of appendages (Figure 3e). Likewise, lowering the  
378 spatial acuity in Scenario 4 did not clearly change the curve trajectory in the transition zone (Figure 3f).



379  
 380 **Figure 3:** Mean Luminance Comparison in experiment 1. (a) The three regions of interest (ROIs) analysed were object region  
 381 (blue), background region (yellow) and appendage region (green). The ROIs were separated by 40 pixels to ensure a clear  
 382 separation of the regions. (b) Scenario 1: variation in appendage thickness. (c) Scenario 2: variation in appendage  
 383 transparency. (d) Scenario 3: variation in appendage length. (e) Scenario 4: variation in background complexity. (f) Scenario 5:  
 384 variation in spatial acuity. Note that the 30 and 72 cpd curves overlap fully.



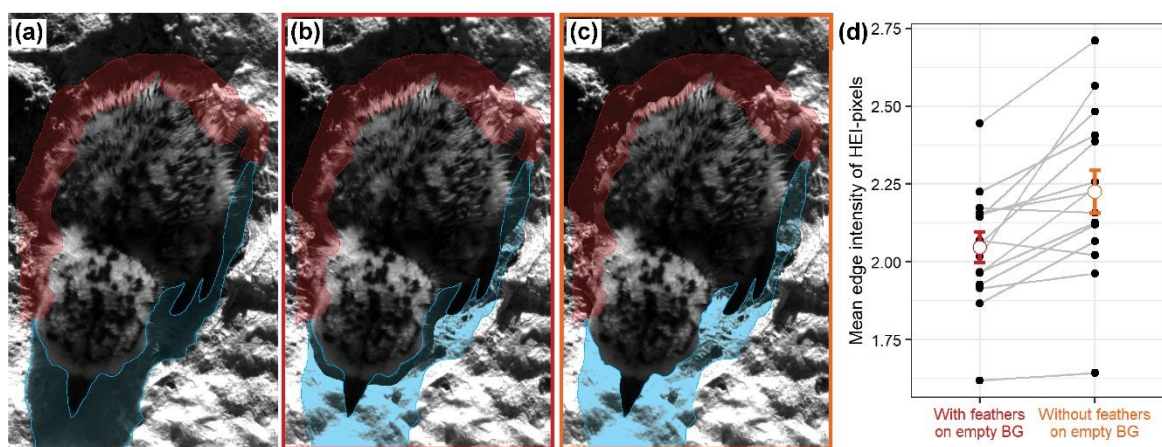
385 Experiment 2: Chick photographs

386 Local Edge Intensity Analysis

387 For eight of the 15 analysed chicks, the empty background image was slightly shifted because of a  
388 camera movement. Therefore, we corrected their position manually to place the chicks exactly at the  
389 same spot in the empty background.

390 After removing the areas of the ROIs where the chick shaded the background, we were able to analyse  
391 on average 72 % of the contour region with LEIA. Across the ROIs of the 15 chicks, the mean threshold  
392 for the HEI pixels was 0.9826 (Table S3). Consequently, we compared on average 1.74 % of the pixels  
393 between photographs of cropped chicks with and without the protruding neoptile feathers.

394 For 13 of 15 chicks (87 %), the mean edge intensities of HEI pixels were lower for the cropped image  
395 of each chick with protruding neoptile feathers (e.g. Figure 4b) than for the corresponding images  
396 without protruding neoptile feathers (e.g. Figure 4c). Accordingly, images including the protruding  
397 feathers showed lower mean edge intensities of HEI pixels than those excluding them (Figure 4d,  
398 paired t-test:  $t = 4.365$ ,  $df = 14$ ,  $p\text{-value} < 0.001$ ). The mean edge intensity difference of HEI pixels  
399 between measurements with and without feathers was 0.178 (95 %CI: 0.091, 0.265).



400  
401 **Figure 4:** (a) A snowy plover chick hiding on the ground from an approaching predator (b) cropped chick transferred to image  
402 of empty natural background with neoptile contour feathers protruding the outline (c) cropped chick transferred without  
403 protruding neoptile contour feathers. The contour region (red) as the region of interest was analysed in the Local Edge  
404 Intensity Analysis. Areas, where the background was shaded by the chick in the original image (blue), were excluded from the  
405 analysis. (d) Mean edge intensity of the HEI pixels in the contour region with and without feathers for 15 snowy plover chicks  
406 ( $t = 4.365$ ,  $df = 14$ ,  $p\text{-value} < 0.001$ ). Measurements are paired by chick ID. The error bars indicate group mean  $\pm$  standard  
407 error.

408 Mean Luminance Comparison

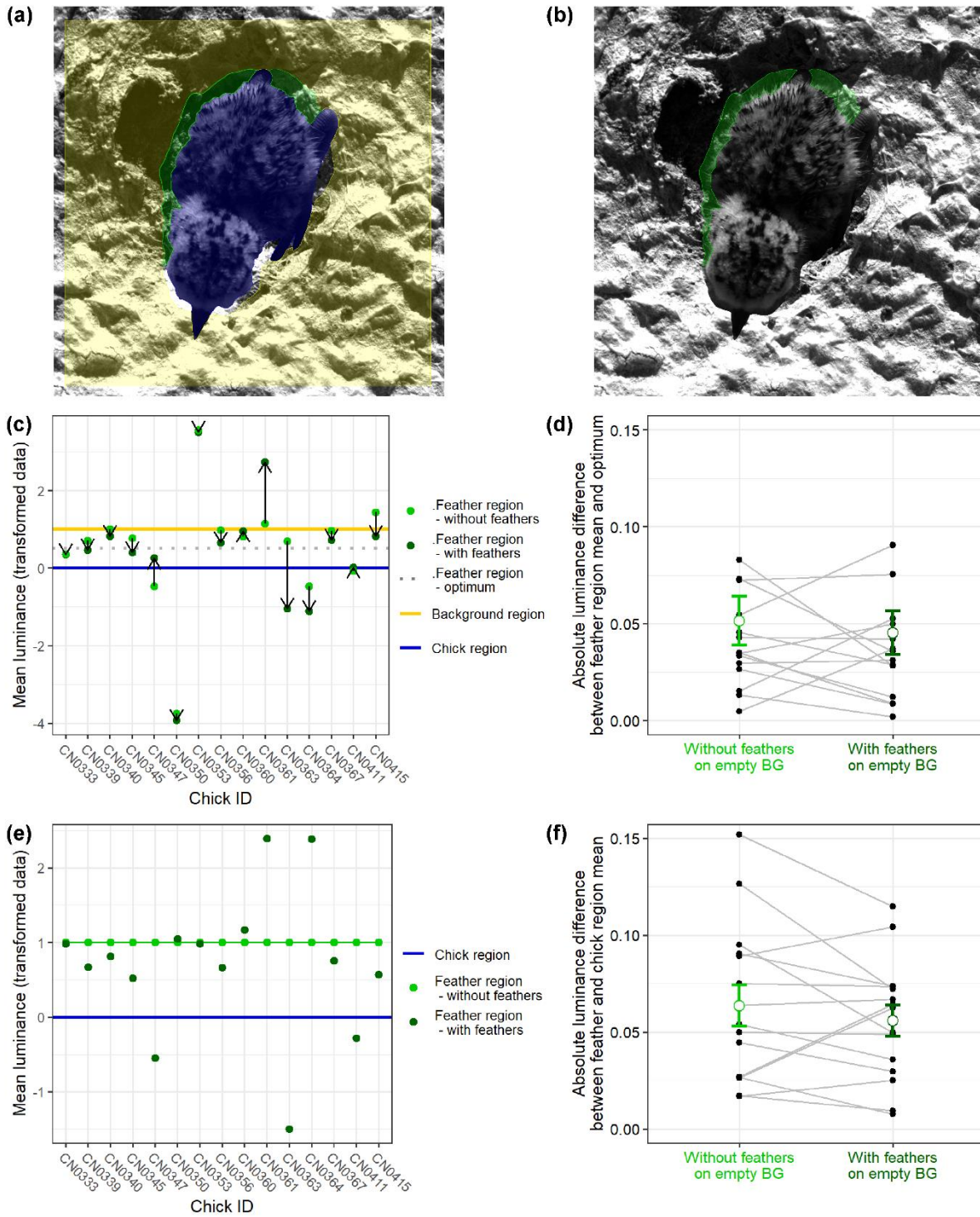
409 For the MLC, presence of protruding neoptile feathers did not contribute to creating a transition zone  
410 between chick and background, as we did not observe more intermediate mean luminance values in  
411 the ROI in comparison to ROI of chick pictures without protruding feathers (Figure 5c-f).

412 After removing the areas that were shaded by the chicks, on average 73 % of the FR remained for the  
413 MLC (Table S3). This value was slightly different from the 72 % that remained of the contour region in  
414 the LEIA because FR and contour region differed in size and the extent to which they were shaded by  
415 the chick.

416 Presence of feathers did not change the mean luminance of the transition zone adaptively. The  
417 distance of the mean luminance of the FR to the optimal intermediate value was in 9 of 15 chicks (60 %)  
418 shorter with than without feathers (Figure 5c-d). The Wilcoxon paired signed rank test showed no clear  
419 difference between the distribution of the two groups ( $p = 0.45$ ).

420 Feathers did not make mean luminance of the FR more similar to the mean luminance of the chick  
421 region. Although the distance of the mean luminance of the FR with feathers to the mean luminance  
422 of the chick region was in 10 of 15 cases (66.7 %) shorter than without feathers (Figure 5f), there was  
423 no clear difference between images with and without protruding feathers ( $t = 1.1263$ ,  $df = 14$ ,  $p = 0.28$ ).  
424 The mean luminance difference between the measurements with and without feathers was 0.0077  
425 (95 %CI: -0.0070, 0.0224).

426 The FR with feathers had an intermediate mean luminance between the chick region and the FR  
427 without feathers in 8 of 15 chicks (53 %) (Figure 5e). In the random sample ( $n = 10,000$ ) from a normal  
428 distribution with the same mean and standard deviation as observed in the transformed data, 38 % of  
429 the values were intermediate between 0 and 1. Including the protruding feathers, we observed a  
430 proportion of 0.53 (95 %CI: 0.27, 0.79) intermediate values, however, this was not clearly different  
431 from expected by chance ( $p = 0.29$ ).



432  
 433 **Figure 5:** Mean Luminance Comparison in experiment 2. The regions of interest (ROIs) analysed were (a) chick (blue)  
 434 background (yellow) and feather region (FR) without feathers (green) measured in scene 2 and (b) the FR with feathers (green)  
 435 measured in scene 1. (c) Measurements were transformed so that the chick region (blue) was always “0” and the background  
 436 region (yellow) “1”. The FR optimum (grey, dotted) portrays the mean of chick and background region. The arrows indicate  
 437 the direction in which the value of the FR was shifted when the feathers were present. (d) Absolute luminance difference  
 438 between FR mean and optimum with and without feathers.\* (e) Measurements were transformed so that the chick region  
 439 (blue) was always “0” and the FR without feathers (light green) “1”. (f) Absolute luminance difference between chick region  
 440 and FR mean with and without feathers.\*  
 441 \*Measurements are paired by chick ID. The error bars indicate group mean +/- standard error.

## 442 Discussion

443 The plumage of newly hatched chicks has several known functions. The feathers are important for  
444 thermoregulation (Wekstein and Zolman 1971). Plumage colour variation is also an important signal  
445 that may reveal chick condition and facilitate individual recognition for parents (Johnsen et al. 2003,  
446 Hill and McGraw 2006, Lyon and Shizuka 2020). In precocial chicks, the plumage provides camouflage  
447 through cryptic colouration (Cott 1940, Hill and McGraw 2006). Here we tested whether neoptile  
448 feathers help to conceal the outline of chicks to make them harder to detect for predators. Our results  
449 from a proof of principle analysis (experiment 1) and analysis of real chick images in their natural  
450 environment (experiment 2) suggest that appendages, such as protruding neoptile feathers, improve  
451 concealment of the object outline, particularly by decreasing the edge intensity. Weak contrast edges  
452 are associated with low conspicuousness (Endler et al. 2018). This enhances diffusion of the outline  
453 and decreases detectability as the shape is an important cue for predators locating and identifying a  
454 prey item (Thayer 1909).

455 In the artificial setup (experiment 1), appendages both reduced edge intensity and created a transition  
456 zone with an intermediate mean luminance in the appendage region suggesting that both mechanisms  
457 help to conceal the object outline. However, when analysing the impact of neoptile feathers on outline  
458 concealment of chicks in their natural background (experiment 2), we found that the  
459 presence/absence of protruding feathers did only change edge intensity but not mean luminance of  
460 the ROI in the predicted way. ROIs on images where the chick was cropped including its protruding  
461 feathers had lower edge intensity but no consistent change in the intermediate luminance was found.  
462 This suggests that the lowering of edge intensity, which we analysed through LEIA (van den Berg et al.  
463 2019) is a better mechanism for outline diffusion than creating a transition zone with intermediate  
464 luminance for concealing the outline of precocial chicks. However, the MLC may be methodologically  
465 problematic for these pictures. Measuring mean luminance across the ROI may not capture the outline  
466 diffusion when both object and background are not monochromatic coloured but consist of a mottled  
467 pattern, which is frequently the case for natural habitats.

468 Altering the characteristics of appendages, background and predator vision had mechanism-specific  
469 consequences. As we concluded that reduction of edge intensity is the more likely mechanism, we  
470 restrict our discussion here to the impact of parameter changes on edge intensity. In the artificial  
471 setup, we found that an intermediate number of regular appendages helped to conceal the outline of  
472 the monochromatic object best. Further, we found that appendage thickness, transparency and length  
473 heterogeneity influenced outline concealment. They altered the optimal number of appendages  
474 needed and, in some cases, changed also the edge intensity. Protruding neoptile feathers of precocial  
475 chicks are thin, somewhat transparent and vary in the extent to which they stand out from the outline.



476 Our results show that thicker appendages would lead overall to higher detectability and in that case,  
477 fewer appendages would lead to better concealment. In contrast, higher transparency required more  
478 appendages for best concealment. Similarly, we found that with increasing length heterogeneity more  
479 appendages were needed to achieve low edge intensities and reduce detectability.

480 Variation in spatial acuity is high across visual systems of different predators and had the largest effect  
481 on edge intensity. Intermediate to high appendage numbers reduced the edge intensity of the ROI  
482 most, regardless of spatial acuity of the simulated predator. Yet, mean edge intensities were highest  
483 for the simulated system with the highest spatial acuity. From the same viewing distance, predators  
484 with high spatial acuity, such as humans or birds of prey, perceive a lot more details of an object  
485 compared to predators with a lower spatial acuity such as canids or corvids (Caves et al. 2018). As  
486 spatial acuity decreases with viewing distance (Caves and Johnsen 2018), mammalian predators need  
487 to approach feathered chicks closer to detect their outline.

488 Interestingly, background complexity did not alter the optimal number of appendages nor impact  
489 overall edge intensities dramatically. Background complexity often makes detection of objects harder  
490 and therefore contributes to camouflage (Dimitrova and Merilaita 2010, Xiao and Cuthill 2016). The  
491 multicoloured fringed feathers themselves could contribute to increasing complexity. Such an effect  
492 would have the largest impact on a more uniform background. The mixture of appendages and  
493 background will also create new false edges and increase disruptive colouration (Troscianko et al.  
494 2017). Nevertheless, any such effects by protruding feathers are likely to be small as the feather region  
495 is only very narrow and, hence, will only impact the immediate surrounding of the chick. Hence it is  
496 unclear whether this effect is biologically relevant for detection through predators.

497 One drawback of our study is that we did not test empirically whether the appendages indeed reduce  
498 detectability by predators, e.g. through a predation experiment (e.g. similar to (Cuthill et al. 2005,  
499 Farkas et al. 2013)). Measuring the detection time of objects with and without appendages similar to  
500 protruding neoptile feathers would be an important test for the relevance of this mechanism in nature.  
501 Concealing the outline is unlikely to be the main antipredator strategy of chicks. We rather suggest  
502 that it works in concert with the cryptic colouration of the downy plumage, chick behaviour such as  
503 finding optimal hiding places and predator distraction or defence through their parents. Yet our results  
504 regarding the spatial acuity suggest that the fringed feathers could be an important component of a  
505 visual antipredator strategy against mammalian predators. Even if the reduction in detectability is only  
506 small, concealing the outline may enhance survival of precocial chicks during early life when chicks face  
507 a very high predation risk (Colwell et al. 2007, Brudney et al. 2013, Eberhart-Phillips et al. 2018),  
508 especially as the costs for having the protruding feathers may not be high.

509 Appendages that alter the outline are commonly found in nature. Examples of vertebrates with  
510 irregular outlines are known, e.g. from cephalopods (Panetta et al. 2017), fish (Allen et al. 2015),  
511 amphibians (Rauhaus et al. 2012) and reptiles (Buxton 1923). A striking example is provided by many  
512 insect larvae such as hairy caterpillars which, as chicks, have typically reduced mobility in comparison  
513 with the adult form. Birds have a strong influence on caterpillar mortality (Campbell and Sloan 1977),  
514 but hairy caterpillars are less preferred prey for avian predators than non-hairy caterpillars (Whelan et  
515 al. 1989). We suggest that concealing the outline might be one currently underappreciated function of  
516 hairy appendages contributing to improved camouflage.

## 517 Conclusion

518 The ‘irregular marginal form’ as a camouflage strategy has inspired early researchers on camouflage  
519 (Cott 1940) but evidence for this mechanism so far has been limited. Our results suggest that body  
520 appendages such as feathers or hairs can help to create an ‘irregular marginal form’ that serves to  
521 diffuse the object outline. Appendages with the characteristics of protruding neoptile feathers reduced  
522 the edge intensity in a proof of principle analysis and on images of precocial chicks taken in their  
523 natural environment. Appendages also served to reduce mean luminance differences when both  
524 object and background were uniformly coloured but this mechanism failed to contribute to outline  
525 diffusion when we analysed images of chicks in their natural backgrounds. Improved camouflage  
526 through outline diffusion could be an important function of heterogenous integuments which are  
527 found in a variety of organisms.

## 528 Declarations

529 Data availability statement – Raw images, data and script are stored in Edmond the Open  
530 Research Data Repository of the Max Planck Society (<https://edmond.mpdl.mpg.de/imeji/>).

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538 Conflict of interest – The authors declare no conflict of interest.



539 Author contributions – VAR, CK and DM conceptualised the study. TV carried out field work.  
540 VAR and CK analysed, interpreted the data and wrote the manuscript. All authors revised the  
541 manuscript.

542 Permits – Fieldwork permits to collect the data were granted by the Secretaría de Medio  
543 Ambiente y Recursos Naturales (SEMARNAT). All field activities were performed in accordance  
544 with the approved ethical guidelines outlined by SEMARNAT.

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