A long tail of truth and beauty: The developmental basis of complexity, symmetry, and beauty in the evolution of the peacock's tail

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ABSTRACT

Darwin's theory of sexual selection based on female choice has become a standard explanation for sexually dimorphic traits such as the peacock's long train. Darwin believed that the peacock's long train has developed as a result of female choice favouring long-tailed mates because of the train's beauty, in which iridescent eyespots play a major role. Female choice theory requires genetic variation in female preference and in the number of eyespots and a genetic correlation between the two, yet there is little variation in either of these traits in natural and feral peafowl populations. We examined the anatomical plan of feather development and found that eyespot feather follicles originate in alternating rows of 10-11; this precludes intrinsic one-at-a-time eyespot variation. The developmentally determined annual addition of new feathers results in a fixed number of total feathers in fully mature individuals. Feather number and coordinated growth of feather length together determine the size of the train, which we propose would have an asymptotic fitness function due to the aging of the male. These results confirm previous speculations that eyespot number may be anatomically determined and complement recent findings indicating that eyespot number alone does not determine reproductive success. We propose an alternate hypothesis: that the driving force behind female attraction and female mate choice is male drive, or male-driven female choice based on male (train) size, quality and vigor, and variation in train display, and not eyespot number. In other words, we propose that, contrary to Darwin's premise, the beauty (eyespot) does not drive the train; rather, it rides the train. The theory proposed here not only provides a simple mechanism for the evolution of the peacock's train, but it also explains past, often contradictory, results. A detailed longitudinal study with cohorts would be ideal to shed light on the details of the process.

INTRODUCTION

The peacock's elaborate train has long represented a paradigmatic case of sexual selection that nonetheless poses a problem for the theory itself because the process whereby the spectacular train of the peacock evolved via sexual selection has to date remained debatable. It has been over 150 years since Darwin recognized the peacock's train as a problem for his theory of evolution by natural selection, a theory that largely accounted for adaptive traits. Darwin was struck by the ornateness of the peacock's tail feathers—the sight of which, as he confessed to Gray, made him 'sick' [1]—but he was also puzzled by the length of the train. Thus, the peacock's train presents two problems: the evolution of train length and the evolution of striking structural complexities in the peacock's upper tail coverts that render it 'beautiful'. As Darwin recognized, the peacock's train was too long to be of much adaptive use—at least to survival, and the tail is hardly an armament used in male-male battles (although we now know that the train can, like the reindeer's antlers, be used in competitive show-offs). Thus, Darwin elected to focus on the beauty of the train and supplied an explanation through sexual selection: that females may prefer to mate with males who possess more beautiful and elaborate trains [2]. This reproductive advantage enjoyed by males with more elaborate trains would compensate for any loss of male survivorship due to predation. This explanation set the stage for research to focus almost exclusively on elucidating how females assess 'beauty' (in peafowl and other birds)[3], thus neglecting other factors, such as male behaviors, development, and physiology.

A key factor required for evolutionary theory, be it via natural or sexual selection, is variation and heritability. If the peacock's train is a target of female choice, then there must be

genetic variation in female preference, which would depend, directly or indirectly, on variation in the peacock's train morphology (size, shape, and/or colouration). Although female choice is widely assumed to be responsible for the evolution of the peacock's train, research on this matter has to date produced mixed results.

Early research suggested that the peacock's train is indeed a target of female choice,as well as an indicator of male condition [4,5]. Whereas one study [6] suggested a correlation between train length and male mating success in wild populations, several studies have suggested that the number of ocelli (eyespots) rather than train length correlates with male mating success in captive and feral populations [4,5,7,8]. A comprehensive 7-year re-evaluation by Takahashi et al.[9] found no evidence that train morphology (either train length or eyespot number) influences the number of copulations a male achieves. More importantly, the re-evaluation uncovered little variation across populations in terms of train morphology, thus calling into question the idea that the peacock's train is a target of female choice. Similarly, in another important study, Dakin and Montgomerie [10] found that males above the age of 4 generally produce between 165 and 170 eyespots before the onset of mating season, and experimentally manipulated males with fewer than 145 eyespots fared poorly in mating. This suggests that there is perhaps a 'threshold' eyespot number required for females to recognize 'normal' and 'viable' mates. More importantly, using their own data and data from the literature, Dakin and Montgomerie found little variation within and between populations in terms of eyespot number [10]. Data from these two studies cast doubt upon the importance of female choice in the evolution of the peacock's train morphology and the nature of variation in the peacock's train. Dakin and Montgomerie[10] quite intuitively suggested that lack of variation in train morphology possibly reflects developmental constraints [11].

The peacock's train is a complex structure, with the upper-tail coverts comprising a diverse variety of feather types, each varying in structure, level of iridescence, colour patterns, and symmetry (S1, see [12,13]for details). The bilateral symmetry of the peacock's train displayed in Fig. 1is quite remarkable (Fig 1): Hundreds of bilaterally symmetrical feathers and eyespots become visible—evenly spaced and arranged in successive rows, not as if on a flat surface but as if in three-dimensional space—from the anterior to the posterior position of the train (Fig 1, also see [10]). The feathers vary in length, with shorter feathers arranged at the front and longer feathers at the back [13]. The peacock's train is thus unique in the sense that a complex trait composed of hundreds of repeating units appears in three-dimensional space and is perfectly(bilaterally) symmetrical. The complexity of the symmetry can be appreciated by connecting the eyespots to one another in any direction (see Fig 2). To achieve this remarkable symmetry in fan formation, the feather follicles must develop in a specific arrangement at their origin, that is, on the uropygium. Indeed, failing to find significant variation within and between populations in terms of eyespot number, Dakin and Montgomerie [10] inspected a male peacock's uropygium and found a constant number and uniform arrangement of follicles, which suggests that train feather development may be genetically and anatomically determined in all males. This developmental constraint imposed by bilateral symmetry raises questions regarding the nature of genetic variation in train morphology and suggests the possible universality of the developmental plan underlying peafowl train morphology.

In this study, we investigated the anatomical development plan of the peacock's train morphology in an effort to penetrate how development may constrain evolutionary elaboration of the peacock's tail. We hypothesized that bilateral symmetry would not enable random variation in eyespots, that is, variation in train morphology arising via the random addition of individual

eyespots in populations. We uncovered developmental and anatomical evidence demonstrating that the nature of bilateral symmetry in the development of the peacock's train feathers would preclude genetic variation in the number of individual eyespots; accordingly, the only source of variation in feather and eyespot number and train size/height would be through the age-dependent addition of new rows of feathers each spring. Thus, all intrinsic between-individual variations may be related to the age of the animals, and, perhaps in all animals, they may reach a developmentally pre-determined limit. This developmental constraint would explain why researchers have not found (genetic) variation in eyespot number in natural populations [9,10]. In this paper, we discuss the implications of these results with respect to Darwin's female choice theory and propose that male behaviour, particularly how males use their trains to establish dominance and to charm females, is an integral, if not the only, component of the force driving the evolution of the peacock's elaborate train.

Fig1. A picture of a peacock tail showing the symmetry of the train and eyespots. Concentric circles enable following the eyespots towards the periphery (picture from Wikipedia/ ThiminduGoonatillake from Colombo, Sri Lanka).

Fig2. Geometrical designs and the symmetry of the train are indicated by dotted lines (above) and their developmental origins in the anchor plate (below). (Peacock picture: from Wikipedia/ThiminduGoonatillake from Colombo, Sri Lanka).

RESULTS

The origin of bilateral symmetry

To allow for reporting the anatomical development plan that determines the bilateral symmetry of eyespots on the train, we examined the uropygium of museum specimens (Royal Ontario Museum, Toronto). Tail feathers are attached to the dorsal, convex side of an oval-shaped uropygium that serves as an anchor plate (Fig 3). The concave, ventral side of the anchor plate exhibits several interesting features:(1) It has basal impressions of tightly packed, parallel rows of feather follicle insertion points; (2) the feather follicles grow progressively larger from the anterior (bottom) to the posterior (top) end and are laid out in alternating rows of 10 and 11 (corroborating the feather arrangement proposed by Dakin and Montgomerie [10]), which 'zigzag' by one position between rows (see Fig 3, right); and (3) the posterior feather follicles radiate in an arch, mimicking the fan formation shape of the train in display. The convexity of the anchor plate renders the train not a flat structure but a three-dimensional structure, such that the feathers are projected outwards at different angles and lengths. It is important to note that the anchor plate itself appears to be a product of continuous growth, sequentially adding new rows of feathers as it grows each spring. The one-to-one correspondence between the impressions of the feather follicle insertion points on the anchor plate and the various symmetrical positions of the eyespots on the train is unmistakable and perfectly matched (Fig2).

Fig3. Left: Anterior portion of peacock tail, showing the newest rows of feathers (at the bottom); Right: Ventral view of the uropygium, depicting alternating rows of 10 or 11 feather cell imprints.

To assess the one-to-one correspondence between the anatomical development plan found on the uropygium and train morphology, we examined several specimens from the Royal Ontario Museum (Toronto) and the American Museum of Natural History (New York).The results are summarized in Table 1 and Fig 4. First, the number of feather rows varied narrowly from 17 to 19, and the anterior 2 to 3 rows had minor eyespots; this is consistent with the findings reported by Dakin and Montgomerie [10]. The minor eyespots only appeared minor because of their slow growth. Assuming that a row of feathers is added each spring, there is technically no upper limit to eyespot number, but these immature eyespots will remain insignificant in their effect.

Second, in the developmental plan of 10/11 feathers per row (reported from 1 individual by Dakin and Montgomerie [10]), they were not arranged in parallel but in a zigzagging arrangement. Moreover, this arrangement appeared to be an invariant trait in our sample (Table 1). This one-to-one correspondence between follicle insertion patterns and train morphology may have been expected, but these data also suggest that the developmental plan does not permit random (one feather at a time) variation in eyespot number (Table 1). We are obliged to report that only a small number of the museum specimens retained an intact uropygium; however, in the data that were available (in 6/21 samples), the 10/11-feathers-per-row pattern was consistent.

Third, the number of fishtail feathers varied around the modal number of 30, 40, or 50, which is what we would expect if fishtail feathers were produced by 3, 4, or 5 rows of feather follicles during development (Fig 4A). This shows that eyespot feathers undergo conversion into fishtail feathers as the animal grows.

Fourth, the number of eyespot feathers varied from 101 to 161, and this variation was presumably attributable to variation between the animals in terms of age, time of year of capture, and some variation due to damage from handling at the museum in the past.

Fifth, there was no relationship between eyespot number and eyespot feather length, except as a function of age. This is consistent with Manning's[12]finding that eyespot number increases during the first 4 to 7 years of the animal's life (see inset in Fig 4B) and thereafter increases more slowly or remains more or less constant (variation in eyespot number in Fig 4B is mostly due to damage).

Finally, there was a strong correlation between the length of the longest fishtail feathers and the length of the longest eyespot feathers($r = 0.97$, $P < 0.0001$), thus the fishtail feathers as a group were invariably longer than and separated from the first row of eyespot feathers underneath them (Fig 4C). It is interesting to note that, while their yearly-sequential appearance on the uropygium may explain some of the variation between eyespot feathers in terms of length, eyespot feathers differ in length, and their growth slows down as the animal ages, inducing asymptotic train growth.

Interspecies variation: *P. cristatus vs* and *P. muticus*

We also had access to a small number of specimens (*N*=7) of *Pavo muticus* (green fowl) from Southeast Asia (Table 1, Fig 4) for comparative analyses, which may provide clues as to whether the peacock's train morphology reflects a similar developmental pattern across taxa or sexual selection and other environmental factors have resulted in different trajectories of train morphology. The *P. muticus* specimens (like all the others) had varying degrees of damage but were still in good enough condition to provide valuable comparative data against the Indian peacock (blue fowl). In the green fowl, the number of fishtails ranged from 38 to 39 (around the expected mode of 42), and the number of eyespots ranged from 115 to 154. As we did not know the age of the animals, we were unable to tell whether these numbers represent upper limits in feathers.

Table 1. Variation between *Pavo cristatus* and *Pavo muticus* in terms of peacock train morphology.

	Feather rows	**Feathers per row**	**Eyespot number**	**Fish tails**	**ESL**	**FTL**
			P. cristatus	(N = 23)		
Mean	18	10/11	129.44	34.42	112.68	134.15
SD	0.63	0	35.70	5.77	25.58	32.17
Range	17 - 19	10/11	101 - 161	24-45	47 - 143	58 – 160
			P. muticus	(N = 7)		
Mean	19*	10/11*	137.50	36.00	101.66	120.16
SD	-	-	14.94	3.52	25.53	29-49

Rage	-	-	112-157	30-40	71-128	85-150

ESL: Eyespot feather length, FTL: Fishtail feather length, * based on one sample only.

Fig 4. Measurements of the peacock's train morphology. Graphs showing the independence of eyespot and fishtail feather numbers (A), the lack of correlation between the(longest) eyespot length and eyespot numbers (B), and the correlation between eyespot length and fishtail length (C). The inset shown in B is after Manning [12] and shows the increase in eyespot number as a function of age. The black bars (A) and black circles (B, C) represent data from *P. muticus.*

The data from both species appeared to be homogenous (Fig4).One green fowl specimen was in pristine condition, enabling us to assess the anatomical development pattern of feather follicle rows in the uropygium. Like feather follicle rows in the blue fowl, the feather follicle rows in the green fowl followed thealternating10/11 arrangement; this suggests that this developmental pattern might be common across peafowl species, reflecting an invariant generic trait across peafowl, although more robust data would be required for confirmation. These data also reinforce the observation that the number of feathers or eyespots cannot be altered one at a time randomly but only in a cohort of 10 or 11.

Train symmetry and complexity

We investigated the significance of the arrangement of feathers in rows of 10/11 and their 'zigzagging' alignment (see Fig 2). To do this, we used graphic design software to reconstruct the unfolding of the peacock's open train based on the developmental layout of the feather follicle insertion points observed in the anchor plate (Fig 5 left). For simplicity, we assumed that the feather follicle insertion points were eyespots without the feather stalks. We then 'modeled' the fan formation in 'display': We subjected the eyespot distribution on the anchor plate to a uniform, bilaterally symmetrical force to spread the eyespots to the left, right, and upward, pushing them radially and uniformly outward in a curved-semicircular space to mimic the fanning pattern of the train during display. Our reconstruction yielded an eyespot distribution that is *identical* to the one seen on the real train (compare Fig 5 with Fig 2): five feathers on either side of the mid-feather in each row. As expected, we found a one-to-one correspondence between the developmental-anatomical layout of the feather follicle insertion points and the symmetrical distribution of eyespots on the train.

Fig5. An illustration of eyespot symmetry showing the layout of feathers on the anchor plate (below) and the resulting eyespot patterns produced by a bilateral symmetrical train (above). The outer spots (green) represent fishtail feathers. Left: 10/11- zigzag feather pattern; Right: 10/11-parallel feather pattern.

We further explored the open-train display pattern to determine whether the feathers were arranged in 10/11 *parallel* rows of feather cells(as presented in Fig 1a in the work of Dakin and

Montgomerie [10]) instead of inthe *zigzag arrangement*. The train-eyespot pattern that we obtained is remarkably different from the 10/11zigzag pattern: Our reconstruction yielded a palm-leaf-like pattern, fanning out parallel rows of eyespots rather than the pattern seen in a peacock's train on display (Fig 5 right). Both patterns are striking, but the 10/11 zigzag arrangement yields a denser and more symmetrical arrangement of eyespots. Most importantly, the difference between the two phenotypic patterns is a basic difference in the spatial arrangement of the feather follicle primordial cells.

DISCUSSION

The main issue concerning the evolution of the peacock's elaborate train (length and beauty) via sexual selection by female choice is *whether females vary in their preferences and whether it is this variation in preferences that is responsible for the evolution of the peacock's elaborate train*. Thus, sexual selection through female choice requires genetic variation in female preference and variation in train morphology. Very little is known with respect to genetic variation in female preference, and one study reported significant levels of heritability in train length but none in eyespot number [14]. Dakin and Montgomerie [10] found that males typically produce approximately 165 to 170 eyespots and that much of the variation in eyespot number is attributable to extrinsic factors. Thus, there is, to date, little evidence of genetic variation in eyespot number in natural populations. In light of our results demonstrating that the developmental plan of caudal feathers does not permit random variation but only permits variation in entire rows of 10 or 11, this is not surprising. Lack of variation in eyespot number, however, is not necessarily evidence against female choice *per se*; it only constitutes evidence

275 *against female choice based* on *eyespot variation*. It also rules out any indirect benefits females
276 may receive if their choice were based on eyespot number. In all likelihood, other factors—such
277 as iridescence of color and/or the bioacoustics of train rattling during display, amongst other
278 aspects of male behavior—are involved [15–17]. Indeed, there is an increasing appreciation that
279 sexual selection operates via multiple signaling cues across taxa [18]. In this case, the peacock's
280 train length[6], eyespot number[4,8,10], the manner in which males use their trains in
281 display[16,17], their auditory signals (hoots) [19], and train rattling[20] cannot be viewed in
282 isolation, nor can they be viewed solely from the standpoint of female choice without
283 considering male behavior.

284 **Development plan and bilateral symmetry limit eyespot variation**

285 Our analyses of the anatomical-developmental layout of the peacock's train reveal that
286 there is a fixed number of feather follicle rows, arranged in a specific pattern of alternating 10/11
287 rows. This appears to be consistent across two species of peafowl. Considering this
288 developmental plan (Fig 3), it is unreasonable to expect mutation to create random variation, that
289 is, add/delete an eyespot. This result is crucial in revealing that the bilateral symmetry of
290 eyespots and the underlying anatomical developmental plan preclude random genetic variation,
291 that is, there is no room for the random addition of one or two feathers to create variation in
292 eyespot number; the only way to create such variation is by adding or removing entire rows of
293 feathers. Thus, as Takahashi et al.[9]and Dakin and Montgomerie [10]found, the small amount of
294 variation that exists within and between populations in terms of eyespot number is due to
295 extrinsic factors such as predation, and so forth. What then, might be the source of intrinsic
296 variation in train morphology?

Lack of intrinsic variation in eyespot number results from constraints imposed by interactions between selection and development and the underlying anatomically determined, fixed number of feather follicles per row of 10/11, which appears to be a threshold trait that varies in terms of row numbers. Thus, the only apparent variation is with respect to growth as the animal ages. As Manning [12,13]suggests, new rows of feathers are added with age. At younger ages (upto4 to 7), rows are added rapidly; the growth rate then declines and eventually ceases, suggesting that a certain number of feathers are added as males reach adulthood, after which addition slows down and is presumably limited to1 row per year. This would correspond with the finding reported by Dakin and Montgomerie [10], who found that most males produce approximately 165-170 eyespots but that experimentally removing around 20 (leaving ~145 eyespots)resulted in males faring poorly in terms of copulation success. On the surface, this would suggest that there is a threshold number of eyespots (>145-150) that is required for females to evaluate as potentially 'viable' an adult male who may deserve further inspection based on other factors; however, as we show below, this interpretation is confounded with the train surface area/height-reducing effect of removing eyespots. This is because a male with~20 eyespots removed from the periphery of the train can be likened to a male who has yet to develop these 20 additional eyespots. Thus, to a certain extent, variation in eyespot number based on age cannot be ruled out as a criterion in the initial stages of mate choice, when eyespot number and train length would be tightly correlated. Both Takahashi et al.[9]and Dakin and Montgomerie [10]found that maximum eyespot number in adult animals is rather invariant within and across populations; this is consistent with slow growth or the complete cessation of new rows of feathers after a certain age.

The relevance of a 10/11 zigzag pattern in eyespot arrangement

Why did the 10/11zigzag pattern evolve instead ofa10/11 parallel pattern? The likely answers to such evolutionary questions assume3 forms. First, the parallel pattern may not be part of the developmentally permitted phenotype space; this does not appear likely. Second, both designs may have been equally likely to evolve, and the presence of one and not the other may simply represent a random 'accident' in evolution. Third, the zigzag 10/11 pattern may have been selectively favoured over the other, perhaps by female choice. An equally likely explanation would be that the zigzag pattern provides more room for individual feathers to radiate freely during train expansion, resulting in an evenly spread but denser pattern of eyespots on a train in display. In the parallel layout (Fig 5), feathers would stack up, one on the top of another, and possibly not only obstruct train expansion and radiation but also diminish the denseness of the eyespot arrangement on a train in display. The contrasting visual difference between the 10/11 zigzag and 10/11 parallel patterns occurs as a result of a small change in the positioning of the feather rows and calls for further investigation into how complexity can arise from small alterations in the basic structural plan.

What do females see in the train?

Although recent research suggests that train length and eyespot number do not by themselves determine female choice, it is curious that experimentally removing 20 or more eyespots from the periphery of the train [4,10] results in males faring worse in terms of copulatory success. By reducing the area of the open train that is covered by eyespots, the removal of ~20 eyespots causes the train to appear 'smaller' (compare Fig 3b with 3c in [10]).

As we surmised above, this apparent ‘reduction’ in train height and the surface area covered by eyespots may be interpreted as signifying a younger male. The reverse, the effect of adding more eyespots, has not been explored but could potentially offer insight into the reality. The iridescence of eyespots appears to be important in mate choice [16], thus the area covered by iridescent eyespots on a spread train may also be important. Considering the apparent lack of a correlation between eyespot number and train length, this presents an intriguing possibility. As the animal grows, the feathers on the back row grow longer, and the eyespots on the outer rims of the train are spread more thinly. This results in a design where the highest eyespot density occurs around the centre of the open train, clustered around the head, neck, and thorax of the peacock (Fig 1). In addition, the rows of long feathers at the back suggest increased selective pressure for length and thickness, which perhaps supply additional support and/or strength during train rattling.

Recent research on visual inspection by females suggests that females selectively scan different areas of the train, as would be expected of any two animals making (visual) contact. One study examining this phenomenon found that females seemed to gaze more at the lower train and areas around the head and body rather than the upper train of a closer peacock but seemed to gaze more at the upper train of a more distant peacock [21]. This would suggest that train length/height and the area covered by eyespots are important to females when judging males from a distance and deciding whether to approach them. In this respect, males with elaborate and longer trains would benefit from being more easily detected by females at a distance. Closer inspection may depend more on iridescence colour patterns and train rattling, amongst other factors [16, 20, 21].

364 **The eyespot structural integrity—an invariant trait?**

365 What, then, maintains the integrity of the spectacular design and colour of individual
366 eyespots? It is worth noting that all the eyespots of a given train are replicas of one another, since
367 they all originated in the same cell; thus, the only variation expected between them, other than
368 environmental variation, would be variation in size due to variation in the age of origin. If
369 females were indeed using eyespots as a criterion for mate choice, this would explain why: Any
370 mutation creating structural alterations would be selected against. The possibility that females do
371 not use individual eyespots as a basis for mate selection, however, warrants equal consideration.
372 Could some developmental mechanism maintain the integrity of the eyespot in the absence of
373 female choice based at least partly on individual eyespots? The developmental control that
374 regulates the train's hue provides some hints. The eyespots of albino peacocks display all the fine
375 structural details displayed by the eyespots of their colourful counterparts. Other colour
376 variations have been observed, and it has been found that the entire animal is typically affected
377 when such mutations occur [22]. Given this finding, it may not be farfetched to surmise that the
378 underlying structural integrity of individual eyespots is governed by the basic developmental
379 body plan that governs the symmetry of the entire animal body.

380 There is a remarkably interesting similarity between an eyespot and the body plan of an
381 animal with the fully expanded train on display (Fig 6). For instance, if the animal with an
382 expanded train is compared to an eyespot, there is a remarkable one-to-one correspondence in
383 overall colour pattern. Indeed, the entire peacock, in full display, body and train, resembles one
384 large eyespot (Fig 1): It boasts a deep blue body surrounded by a dense zone of bluish-green
385 eyespots, which corresponds to an individual eyespot with its deep blue inner circle surrounded

386 by radiating oval rings of mixed colours. Pending more technical clarification, to the best of our
387 visual inspection, while the outer circles of the eyespot may vary, the innermost area is, like the
388 deep blur thorax and head of the animal, consistently a deep blue colour. We conjecture that the
389 eyespot is not a terminal structure that evolved with the iridescence of varying colours but is a
390 terminal structure of the basic body plan of the animal. More specifically, the colour patterning
391 of the animal may be determined by the same developmental circuitry as the colour patterning of
392 each individual eyespot. This may also explain why eyespot structure appears to be invariant
393 across peafowl species. Further research is required to test this speculation.

394

395 **Fig 6**. Correspondence between the eyespot and whole animal body plan: The turquoise blue
396 body of the peacock, which is surrounded by a green area, corresponds to the dense dark blue
397 area of the eyespot, which is surrounded by layers of various colours.

398

399 **Sexual selection theories**

400 Sexual selection theory is characterized by a colourful, controversial history. Notable
401 examples include Darwin's principle of 'female choice' based on 'good taste', Wallace's
402 principle of 'good sense' based on natural selection, Fisher's 'run-away' and 'good-taste-makes-
403 good-sense' principle, and Zahavi's 'good-genes'-based handicap principle [2,23–25]. Darwin
404 used female selection based on the train's 'beauty' as an example to illustrate a continuum
405 between human and non-human animals with respect to aesthetics and appreciation of beauty.
406 Fisher came to Darwin's rescue by invoking the co-evolution of female 'choosiness' and the long
407 tails of males. Given an inexhaustible amount of genetic variation, this scheme can potentially

engender a ‘runaway’ process producing accelerated change. Female choice can be based on any trait—eyespot number, iridescence of eyespots [16], or train rattling behaviours [20]—provided that it spawns variation and is correlated with train size.

Our data and data provided by recent studies, particularly the studies conducted by Takahashi et al.[9]and Dakin and Montgomerie [10], highlight some issues with the generally assumed universality of female selection and its targets in males. Nevertheless, alternatives to female selection are rarely entertained. Below, we briefly review two major versions of female choice theory and provide an alternative, but by no means mutually exclusive, male version: the theory of male drive.

Standard female choice theory

Darwin’s female choice theory is based on ‘beauty’, and the eyespots are commonly deemed the target of female choice. Standard female choice theory also relies on the assumption that eyespot number and train length are correlated and that female choice based on eye spot number will lead to the correlated increase in train length. The results of this study and others [9,10], however, suggest that eyespot number is anatomically determined and invariable and thus cannot be the sole factor driving the evolution of the peacock’s elaborate train. Nevertheless, there is a possible scenario in which eyespots could become the basis for selection. Given that train feathers are added in rows of 10 or 11andare added rapidly during the first 4 to 7 years of a peacock’s life [12], eventually reaching 150 to 170 at adulthood, and given that feather number and length determine the elaborateness of the train (size and eyespot number), it follows that any variation in growth rate, that is, the rate at which feather rows are added, could be subject to

430 selection if the size of an open train were a direct or indirect criterion directing female choice. As
431 such, rapidly growing males may develop more elaborate trains (size and eyespot number) and
432 may become preferential targets of female choice during the peak period in the first 4 to 7 years
433 of life, after which feather number may still increase but at a slower rate [12](Fig 1).This would
434 explain why train length and mating success appear uncorrelated in contemporary populations of
435 mature/old individuals. The scenario we describe would apply to the robustness of the male
436 during the growing phase and upon reaching adulthood with the full complement of feathers, as
437 opposed to those that are lacking in this regard.

438

439 **Composite female choice theory**

440 The various scenarios that have been proposed for female choice raise the possibility of
441 'beauty and brightness' working together to affect tail length either directly based on beauty
442 [2,23,26] or indirectly based on fitness [24] or parasite load [27]. The male trait under female
443 selection need not be eyespots alone but could potentially be a composite trait incorporating
444 many aspects of male morphology—such as eyespots, color, iridescence, train size, and shape—
445 and male behaviours. This composite trait, or 'beauty', could be proportional to the size of the
446 train, which could also depend on the nutritional condition of the male. The problem with this
447 model is that, while the effect of the composite trait might increase as a function of increasing
448 train size, its effectiveness will decrease and undergo dilution as the train increases in size. It is
449 important not to confound the mechanism through which female choice theory operates to
450 account for exaggerated secondary sexual traits and the way in which females choose their mates
451 in general based on composite cues, including mate recognition traits. Furthermore, it is

important to note that the more composite the nature of the female choice, the greater the likelihood that it is driven by male behaviour. Since the major component of train size (height) stems from feather growth (length) rather than eyespot number, it follows that the elaboration of the train is not driven by beauty. Moreover, it is, if anything, the other way around: Beauty depends on how elaborate a train is and how it is used, which should depend on the developmental status and vigour of the male. In the following, we provide such a theory of male-driven evolution.

Male drive or male-driven female choice

Darwin emphasized how active males are in the mating ritual [2]. Males engage in male-male competition, or they engage in energetic visual and auditory displays to 'charm' females. Although Darwin noted the heightened activity of males during breeding season, he did not consider that all males are alike in one respect, that is, they are all driven by what we denominate male sex drive [28], or male-driven sexual selection. This essentially concerns the way in which males leverage their resources—ornaments, armaments, physical condition, vocalizations, and so forth—to succeed in attracting mates. Dakin et al.[16,17,20] highlight such male behaviours, although they eventually attribute mating success to female choice alone. Dakin and Montgomerie [16,17]demonstrate how males orient their train display at specific angles to the sun to maximize the iridescence of their eyespot colours. It would be useful to document whether any inter-male variation exists in such behaviour. Males may utilize their train morphology and the environment (including lek territory, angle of the sun, etc.) to maximize the effectiveness of their displays. In addition, train rattling behaviours almost always precede copulation and appear important in mate choice [9,20]. Dakin et. al.[20]elucidate how the male condition, particularly

its mass and energetic conditions, facilitates train rattling efficacy and the resulting bioacoustics during train rattling. All males are not created equal: Male behaviours are variable and are themselves under selection, from both natural and sexual selection.

Males display their trains to rivals; they do not rattle their trains, but train displays have been shown to form part of male-male aggressive behaviours, thus informing males' assessments of rivals [29]. In this respect, size would count, and larger would be better. For instance, train displays perhaps help males to attract the attention of females from a distance [21], in which case train length would certainly signify. When females are nearby, males engage in their courtship displays, using train rattling and wing shaking, orienting their trains at certain angles to the sun, and engaging in run-and-hoot behaviour [4,9,17,20]. Interestingly enough, Yorzinski et al.[29]demonstrated that peacocks assess rivals using cues similar to the cues that females use to assess males. One study found that females spent more time gazing at the lower train, which is lined with eyespots and fishtails, and the body during courtship displays[21];meanwhile, another study found that males spent more time gazing at the lower train eyespots and fishtail feathers and the body and wings of rival males[29]. This strongly suggests that the traits used in courtship displays are also used to assess rivals [30].

These data highlight an important and long neglected point in explaining the evolution of male sexual characters: Sexual selection is an interaction between male behaviours and female assessments of male behaviours. Indeed, the evolution of some characters, such as iridescence [16], may have been driven by female preference, but other aspects of train morphology, such as train size and how males use their train, cannot be explained by female choice alone. Indeed, teasing the two apart is an enormously challenging task, but, as Takahashi et al.[9]discuss,

496 researchers need to seek alternatives to female choice, especially when data suggest that such
497 alternatives are required.

498 Male drive theory does not discount female choice; it only suggests that train
499 morphology—as a result of successive annual additions of rows of new feathers, as a function of
500 the male condition, which perhaps reflects dominance—drives female choice, either directly,
501 through sensory capture [31], or indirectly, through colour patterns and beauty-based mate
502 choice or mate recognition [32]. Table 2 provides some insight into the possibility that several
503 observations can also be explained by male sex drive, which may trigger female preferences.

504

505 Recent comparative analyses of the peacock genome have revealed adaptive evolution of
506 genes controlling skeleton-muscular and feather developmental pathways. Further
507 interdisciplinary research will be required to determine whether this has occurred due to female
508 choice or male drive or, more likely, an interaction of the two. Our analyses, however, indicate
509 that the anatomical developmental layout of caudal feather follicles is uniform and consistent
510 across two species of peafowl and that this developmental layout does not enable random
511 variation in feather number. Thus, past sexual selection may have favoured increased eyespot
512 number and train length, amongst other morphological traits of the peacock's train. Given how
513 males use their trains in rivalry and in courtship, however, female choice is unlikely to have been
514 the sole selective pressure directing the evolution of the peacock's elaborate train. Alternatives
515 invoking male behaviours alongside female responses will be required to achieve a complete
516 understanding of how sexual selection has operated in the evolution of the peacock's train.

517

518 **The law of diminishing returns and asymptotic fitness function**

519 The excessive length of the peacock's train and the likelihood that it would expose the
520 animal to high predation has been a major argument against its adaptive value. Negative
521 selection is expected to function as a constraint against further lengthening. The pattern of
522 feather development and growth reveals that the tail has a self-limiting growth pattern, possibly
523 for another reason that is unrelated to predation.

524 The relative length of the train is a function of both feather number and feather length.
525 After 4 to 6 years of rapid growth [12], the rate of addition of feather rows slows down.
526 Furthermore, the newly added feathers grow very slowly (Fig 3). This suggests that after a male
527 has reached his peak reproductive age and accrued the threshold number of eyespots to have
528 started mating, his mating success will increase as a function of both the size and quality of his
529 train and his vigour in mounting a display. Since the overall vigour will begin to decline as the
530 animal grows older, the fitness function will plateau and ultimately decline in spite of train size.
531 At this point, the *law of diminishing returns* will infect tail length or train size, and each
532 additional row of feathers will grow slowly and exert only a minimal effect on the fitness of the
533 male. This would explain why later additions of feathers grow very slowly. The limitation with
534 respect to maximum eyespot number and the lack of correlation between train length and mating
535 success may, as suggested by Takahashi et al. [9], indicate that these traits have reached a
536 threshold. The asymptotic nature of the fitness function would explain a number of aberrant
537 results, such as the inconsistent correlation between train length and eyespots and success in
538 copulation.

539

Conclusion

Sexual selection theory suffers from 4unquestioned basic assumptions. First, Darwin assumed that there are two kinds of males: those who fight, such that the winners claim the females, and those who engage in dance and display, such that the female is afforded the opportunity to choose whom she mates with. Darwin was so impressed with the peacock's dance and display that he failed to notice that the functional role of the tail resides in the unfurled train, which accentuates the peacock's size when displayed, perhaps even suggesting dominant status. Moreover, a larger train can attract females from a distance. In this respect, the peacock's train is no different than the reindeer's antlers. Second, Darwin assumed that the train's beauty drives train length through female choice, without any evidence that the two traits were correlated. Third, all animals have their own species-specific *mate recognition* system, which can often be confounded with *mate choice*. Exaggerated, bright, and beautiful traits often form the basis of both. Finally, in striking cases of 'sexually selected traits', the female choice theory has been taken for granted, and a series of follow-up theories have been developed to illustrate not how but why females choose. All of these assumptions apply equally to the case of the peacock's train.

Thus, alternatives have rarely been explored: All the proposed theories of sexual selection's decisive role in the evolution of the peacock's train are variations on the same theme, female choice, and research has focused on the basis underlying female choice based on aesthetics and beauty [2,26,33], the handicap principle [24], or parasite load [27]. Even the age-advertisement theory [12,13],which threatened to entertain an alternative to female choice,

562 succumbed to female choice by proposing that females prefer older males because they have
563 demonstrated their genetic quality by surviving an array of selective pressures. Should that not
564 apply to all old males in the context of all organisms?

565 Our results substantiate some theories and observations and refute others. First, our
566 observation of alternating rows of 10/11 feathers in the train supports the suggestion of Dakin
567 and Montgomerie [10]that eyespot number is internally determined. The internally determined,
568 fixed number of eyespots explains why many previous studies have failed to find significant
569 variation in eyespot number. Second, our results substantiate the observation of Takahashi et al.
570 regarding the lack of a correlation between train length and mating success and their conclusion
571 that eyespot number and train length have reached their limits and are no longer under selection.
572 The lack of a correlation would follow from the asymptotic fitness function and the low mating
573 potential of larger but older males. Third, our results provide an alternate explanation for age-
574 advertisement theory [12] by proposing that it may not be the older males but the larger trains of
575 the older males that females may prefer over younger males, who continue to grow and increase
576 their train size and mating potential. Fourth, for the first time, our results provide an alternative
577 to female choice theory by proposing that train morphology *is also* under selection as a result of
578 male drive or male dominance (Table 2, Fig 7). We propose that train size (meaning male
579 dominance status) is the basis of female choice, which in turn drives train size. Finally, we
580 further propose that, while eyespot number may be the basis underlying attraction and mate
581 recognition, it is not the basis underlying female mate choice, as it is not correlated with train
582 growth. In addition, there is to date no evidence to support variation in female choice; however,
583 variation in female preference is required for Fisher's runaway selection, not for the evolution of
584 long tails.

585

586 **Fig 7.** A demonstration of the steps involved in the development of the peacock train and sexual
587 interaction, including behavioural response and selection pressure.

588

589 Our aim here is not to discount female choice theory, as more research is needed to test
590 its validity. Our aim is to propose that even under the best circumstances for female choice,male
591 drive, or male-driven sexual selection, should be entertained as an alternative, or even as the null
592 hypothesis. One cannot, as Darwin did, divide males into two groups of fighters and dancers. All
593 males live by Bateman's principle [38], have been selected for sexual drive [28], and vigorously
594 pursue mates.Ornaments can be used as armaments; dances can be interpreted as displays of
595 dominance, quality, or even coercionin the eyes of the receiver.

596 Mate choice makes for good mythology. The power of female choice is depicted in
597 Indian mythology through Hindu God Krishna wearing a single peacock feather in his crown
598 while being chased by his beloved devotees, and the power of the male sex drive is represented
599 by Shiva, the Nataraj (Lord of dance), known for his legendry beauty and virility. Shiva has no
600 need to borrow charm from the peacock's charm: During his birthday celebrations, young
601 women flock by the thousands to the Temple to seek his blessings for good future consorts.

602

603 **Table 2.** Explanatory power of female choice versus male sex drive

Study	**Finding**	**Explained by**	
		Female choice	**Male sex drive**
(Petrie et al. 1991,[4]; Loyau et	Number of successful copulations increases	Yes	Yes

al. 2005,[34])	with eyespot number		
(Yasmin and Yahya 1996,[6])	Mating calls correlated with mating success Longer train correlated with mating success	Yes, MR Yes	Yes, MR Yes
(Manning1989,[12])	Eyespot number related to age; a peahen may choose older males	Yes, MR	Yes, MR
(Manning 1989,[12]; Petrie et al. 1991,[4])	Males rub feathers and produce rustling noises to attract females	Yes	Yes
(Manning and Hartley 1991,[13])	Symmetry of train increases with eyespot number -	No	No
(Petrie et al. 1991,[4]; Loyau et al. 2005,[34])	Longer train not correlated with mating success Number of successful copulations increases with eyespot number	No Yes	Yes Yes
(Petrie 1992,[35])	Probability of predation negatively related to eyespot number	Yes	Yes
(Petrie and Williams 1993,[36])	Female egg production related to train length	?	Yes
(Petrie et al. 2009,[14])	Eyespot number not related to body mass or muscle size	No	No
(Petrie et al. 1991,[4]; Dakin and Montgomerie 2011,[10])	Removal of 20 eyespots decreases number of successful copulations	Yes, MR	Yes
(Pike and Petrie 2005,[37])	Biased sex ration when female mated with male with20 eyespots removed	No	No
(Loyau et al. 2007,[8])	Female egg investment increases with eyespot number	Yes	Yes
(Loyau et al. 2005,[7])	Faster immunological recovery with greater eyespot number	Yes	Yes
(Takahashi et al.	Number of successful copulations not related to eyespot number	No	Yes

2008,[9])			
(Dakin and Montgomerie 2011,[10])	Mating success not related to eyespot number Removal of 20 eyespots decreases mating success	No No, MR	Yes MR
(Dakin and Montgomerie 2013,[16])	Ocelli colour correlated with mating success	Yes	MR
(Dakin and Montgomerie 2014,[19])	Special mating calls (hoots) attract females	MR	Yes, MR
(Dakin and Montgomerie 2009,[17])	Peacocks use angle of sun to orient their displays	No	Yes
(Dakin et al. 2016,[20])	Bioacoustics of train rattling display	Yes	Yes

MR = Mate recognition trait

607 # MATERIALS AND METHODS

608 ## Peafowl specimen

609 The data presented in this report are based on observations of the tail structures of
610 museum specimens kept at the Royal Ontario Museum, Toronto and the American Museum of
611 Natural History, New York. In all the available museum samples, there were varying degrees of
612 damage, from damaged to missing eyespots. Only specimens in reasonably good condition were
613 included in this study. In total, 23 samples of blue fowl (*P. cristatus*), including 2 albinos, were
614 examined. The blue fowl samples originated in the wild in India (n = 3), Ceylon (n = 2), and
615 Nairobi (n = 1) and in parks (captive samples) from the United States (n = 4 blue, n= 2
616 albino).The remaining 11 were of unknown origin; this included 2 hybrids,1 of which was
617 identified as the product of mating between individuals originating in Bangkok and Cameroon.
618 We also had access to 7 samples of green fowl (*P. muticus*) at the Natural History Museum;
619 these samples originated in Malaysia (n = 4) or Bangkok (n = 1) or were of unknown origin (n =
620 2). Wherever dates were noted, most of the field samples were collected during the early part of
621 the1900s; the captive samples (United States), conversely, were collected as recently as 1942.

622 ## Data collection and measurements

623 We counted the number of eyespots, eyespot feathers, and fishtail feathers displayed by
624 each specimen. The length of the feathers was measured from the base to the top of the feather
625 for eyespot and fishtail feathers. In the cases where an eyespot was missing due to damage, we
626 counted it as if it had an eyespot for the purpose of estimate the total number of eyespots. Very
627 few of the samples had uropygium in good condition. Wherever we were reasonably sure that the

integrity of the sample had not been compromised, we counted rows of feather imprints on the uropygium.

Developmental simulations

We used Adobe Illustrator's inbuilt features to create a model of the eyespot symmetry exhibited by trains in display. Briefly, Adobe Illustrator was used to map concentric circles following eyespot distribution on the train in display, using Figure 1 as a template. These sets of concentric circles were used as a basis for text paths determining how the eyespots may distribute themselves on the unfolding of the train for display.

To simulate the train's eyespot distribution, we represented train feathers with a dot row of 10 or 11 in the shape of a uropygium. In line with our observation (Fig 1), we increased the spacing between rows by a constant factor between the rows progressively, from the bottom (newest) to the top (oldest) feathers. We simulated 2 spatial arrangements, a zigzag alternating arrangement and a parallel arrangement, of 10/11 feathers (Fig 5). The feather grid was expanded symmetrically to the right and to the left to mimic the animal's train expansion.

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Supporting information

S1: Peacock's tail—structural complexity and symmetry

Structure: The peacock tail is a complex trait consisting of various kinds of feathers and eyespots with varying densities, arrangement patterns, and colours. The train consists of 2 traits. One is the tail's overall size, composed of a large number of feathers spread radially, resulting in a nearly 180-degree spread-out fan (train). This fan formation now records a radius, a height, and an area that correspond to tail feather length. The other trait is the eyespot number, which can vary from small to large, from anterior to posterior.

Feathers: The train consists of rows of feather laid down from front to back (anterior to posterior), from the youngest and smallest to the oldest and longest. The feather shafts are cylinders filled with foam, robust and flexible[38]. As we move from anterior to posterior, the spread of the eyespots becomes progressively wider and thinner in density, suggesting that the back-row feathers grow faster, pushing the eyespots outwards. The faster growth of older feathers at the top of the train and towards the sides exerts a flaring-up/expanding effect,

749 rendering the feather insertion points (outlined as white diamond outlines in Fig 2) progressively
750 larger towards the top and the sides of the tail. The anterior, basal part of the tail exhibits rows of
751 newly arisen small feathers, each with a complete circular blade but with an incompletely filled
752 eyespot, as determined by examining the shorter, 'newer' tail covert feathers. The eyespot
753 colours appear to grow from the 'inside-out', originating in the centre of the eyespot and
754 radiating as the blade grows. The eyespot colours become fully developed by row 3 (from
755 anterior to posterior).

756

757 **Eyespots:** Eyespot number in natural populations varies from roughly 165 to 170, with a mean
758 and range from 139 to 160 and from 110 to 167, respectively[10]. The Maximum number can
759 potentially reach200 (this study). Because each feather develops only one eyespot, the total
760 number of eyespots is dependent on the number of feathers. Not all feathers develop eyespots. A
761 significant number of back-row feathers (3-4 rows) develop a fishtail structure (Fig 1), and a
762 minority develop minor eyespots or side swords. Variation in eyespot number is not attributable
763 to variation in body condition or the extent of train growth among males.

764

765 **Symmetry and beauty:** The peacock's train has perfect bilateral symmetry, and in each half, as
766 one moves away from the train's centre, towards the sides, the feathers become progressively
767 longer, which means that the tail is not a perfect half-circle (Fig1). If we place the whole 'animal
768 body' at the centre, however, the tail appears as a nearly perfect half-circle (not shown). In
769 addition to bilateral symmetry, the eyespots appear perfectly placed in a geometrical three-

770 dimensional structure from all sides, suggesting an underlying developmental-anatomical plan
771 (Fig2).
772
773 **Developmental design and origin of eyespot symmetry:** The basal, ventral side of the tail
774 shows its feathers to be anchored—in alternate rows of 10 and 11, from the youngest, anterior,
775 rows to the oldest, posterior, rows—to a plate that is oval, convex, slightly bilaterally curved, and
776 symmetrical, aligning with the bilateral spread of the train. The older rows of feathers show
777 progressively larger feather imprints on the anchor plates, suggesting the development of thicker
778 feathers as the animal ages. All aspects of symmetry—the semicircular spread of the train, the
779 symmetry of the eyespots, and the horizontal radius and its tapering off towards the end on both
780 sides—can be structurally explained in terms of the developmental design of the feather anchor
781 plates.
782

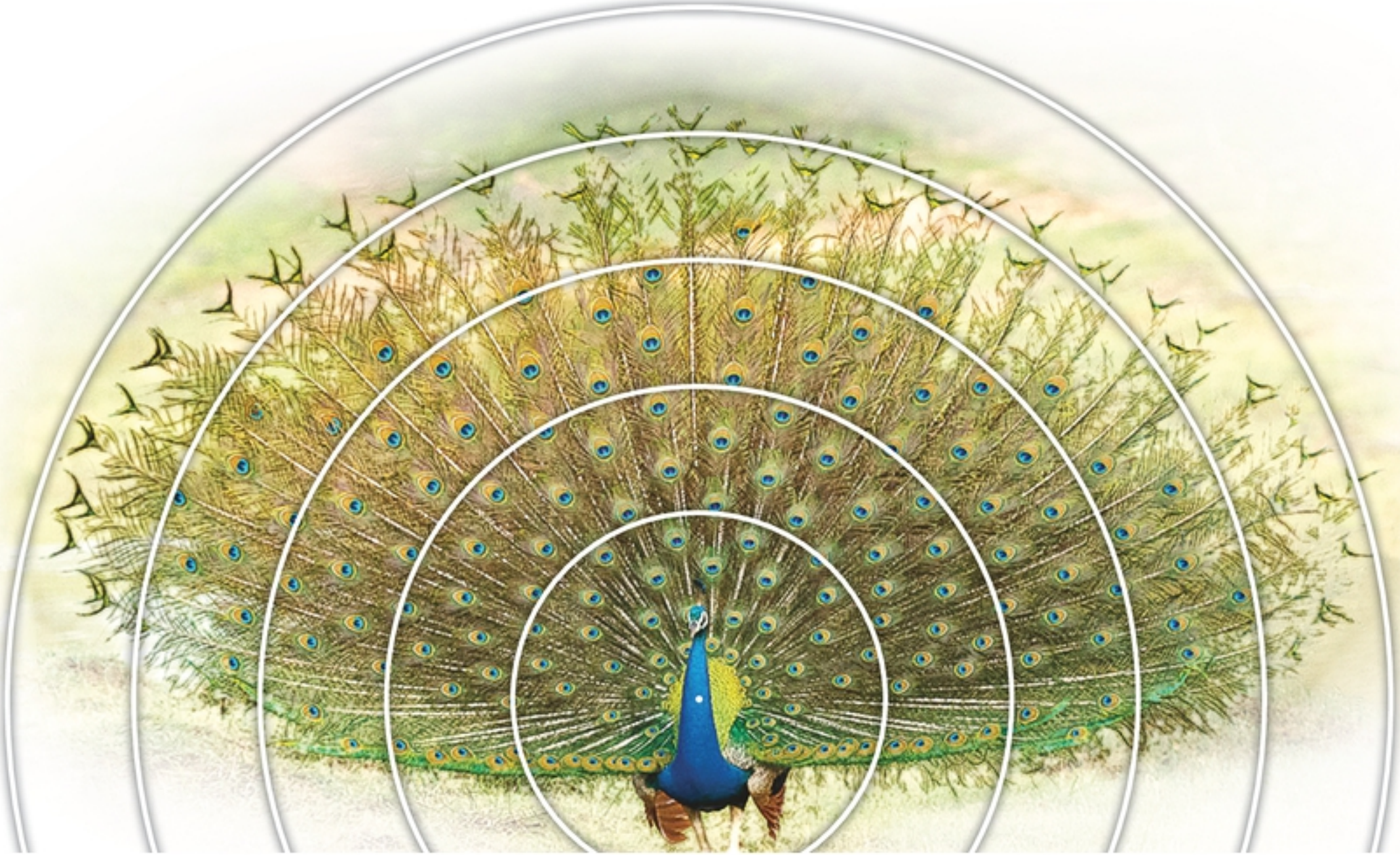

Figure 1

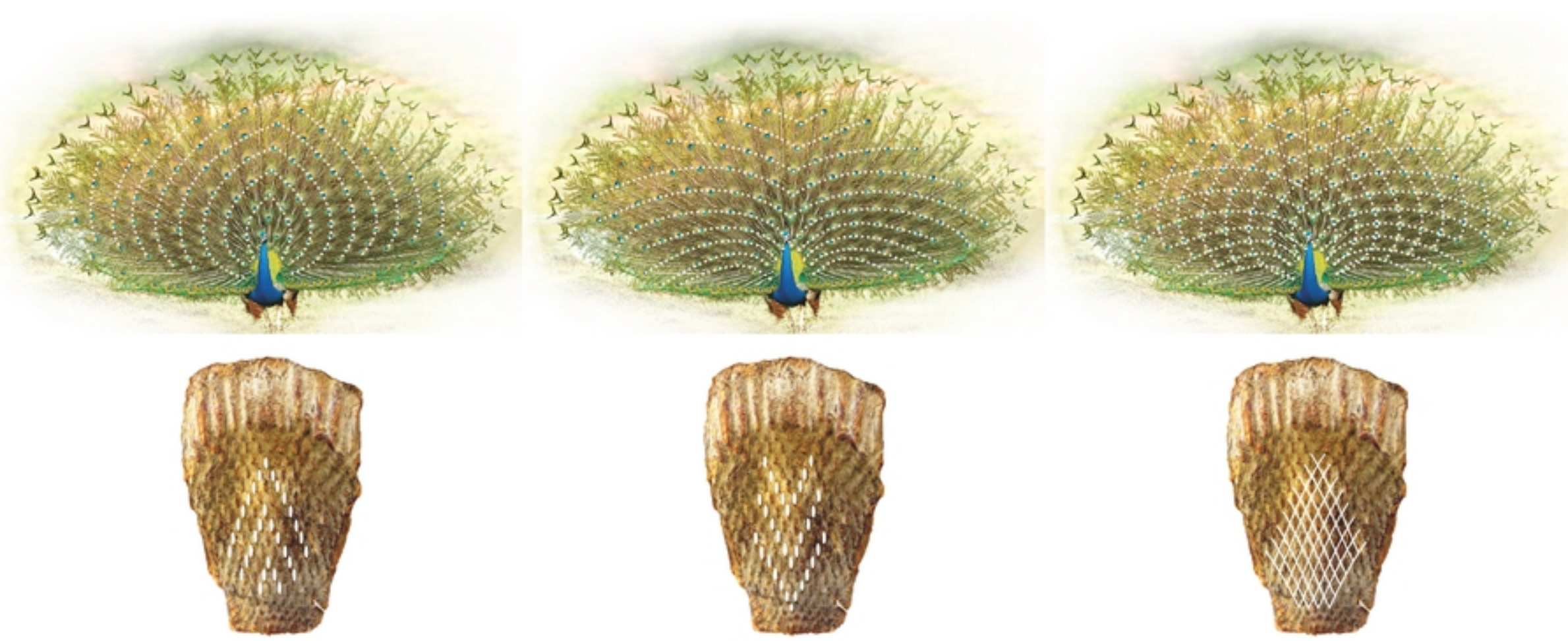

Figure 2

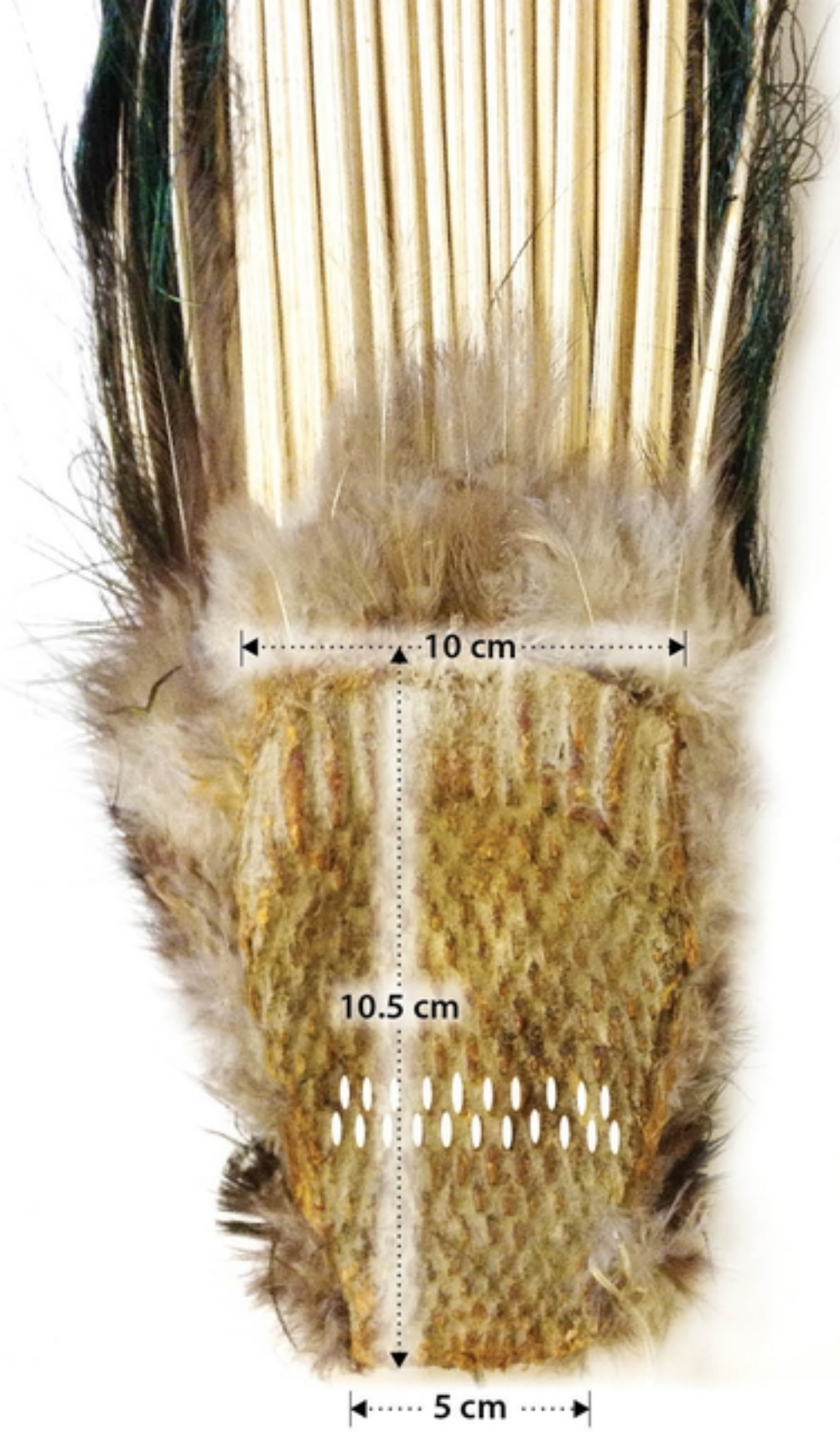

Figure 3

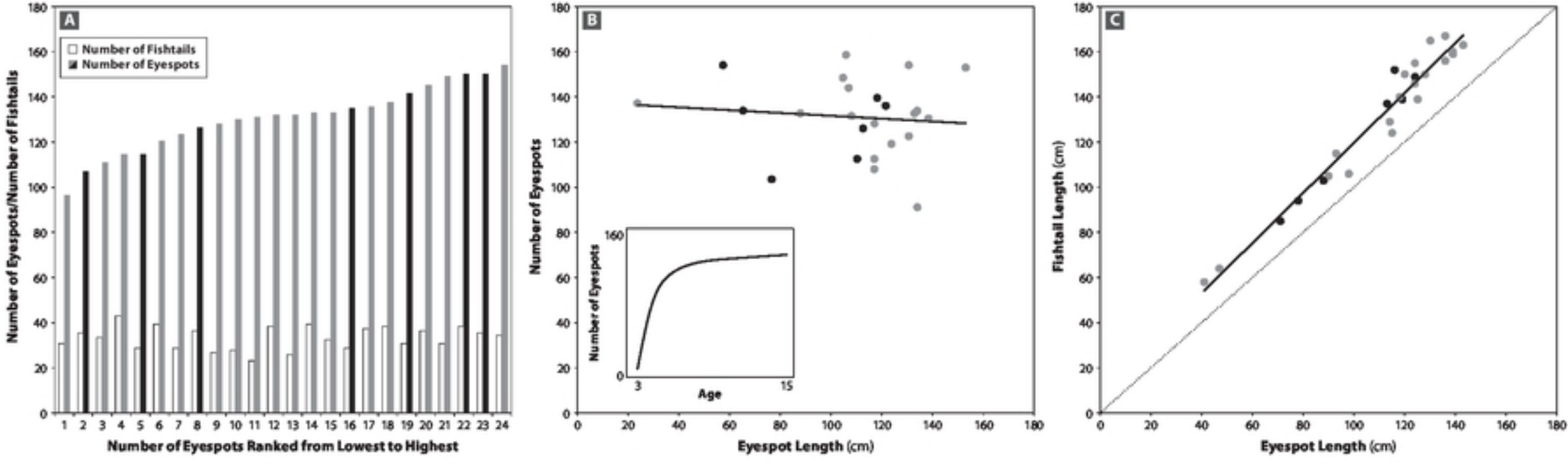
A
Number of Fishtails
Number of Eyespots
Number of Eyespots/Number of Fishtails
Number of Eyespots Ranked from Lowest to Highest
B
Number of Eyespots
Eyespot Length (cm)
Number of Eyespots
Age
C
Fishtail Length (cm)
Eyespot Length (cm)

Figure 4

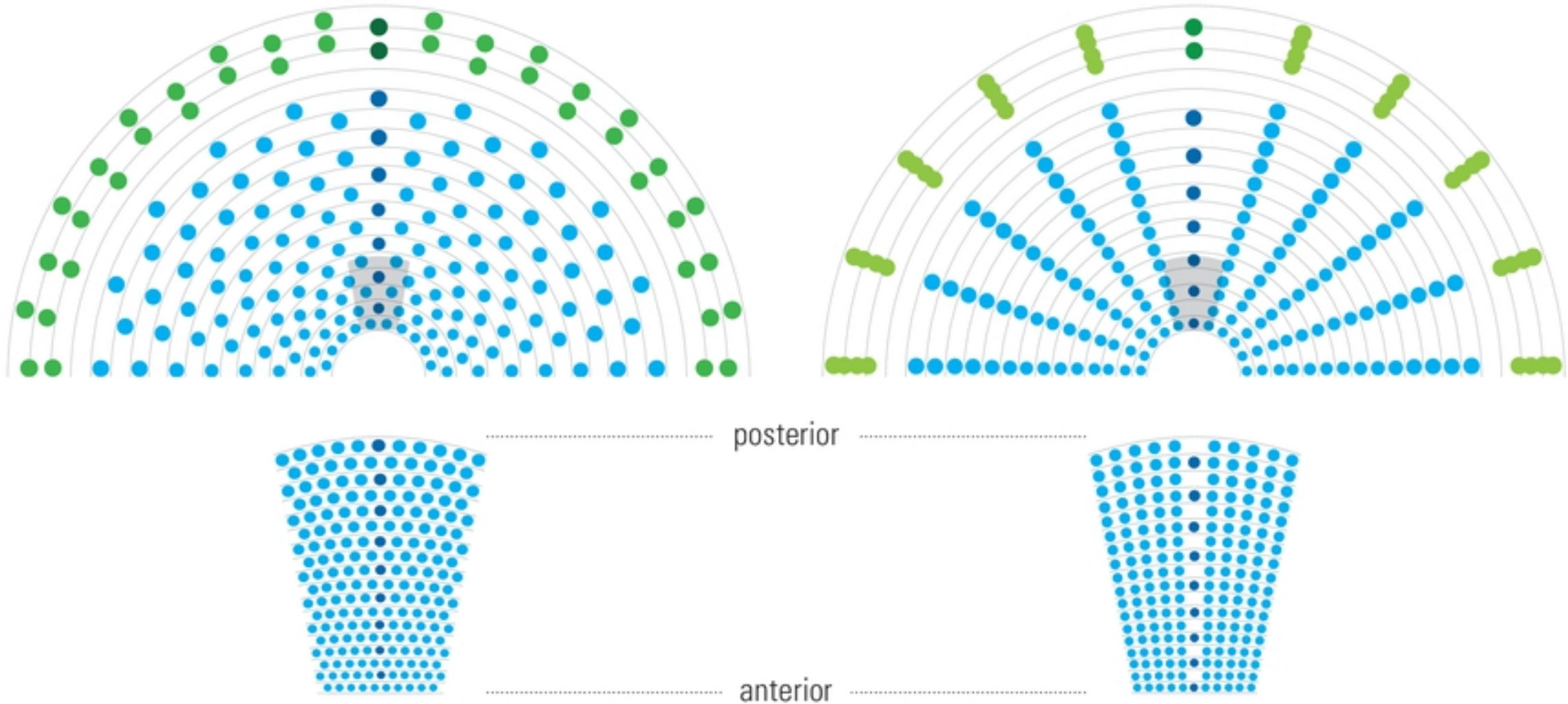

Figure 5

Figure 6

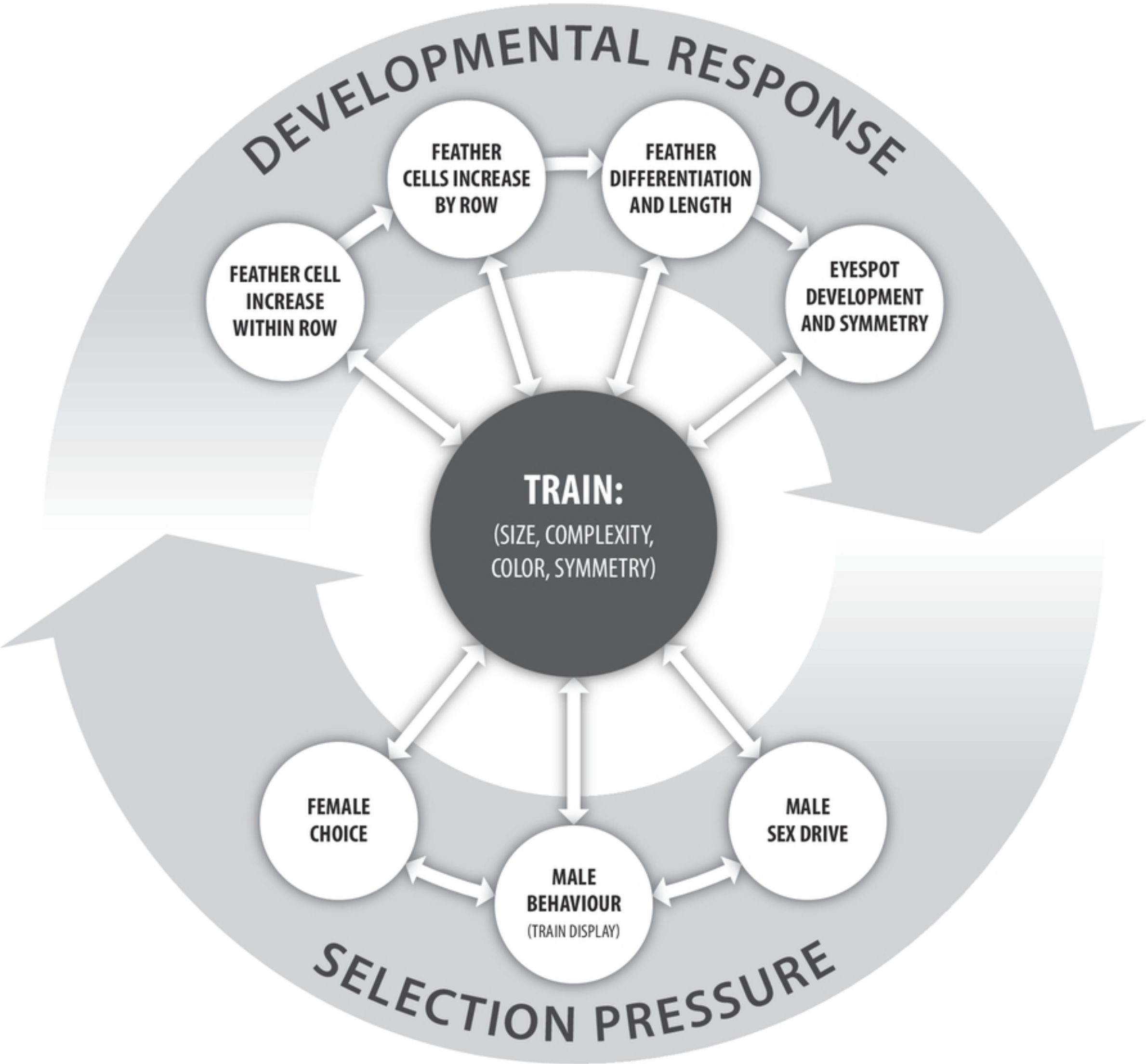
DEVELOPMENTAL RESPONSE
FEATHER CELL INCREASE WITHIN ROW
FEATHER CELLS INCREASE BY ROW
FEATHER DIFFERENTIATION AND LENGTH
EYESPOT DEVELOPMENT AND SYMMETRY
TRAIN:
(SIZE, COMPLEXITY, COLOR, SYMMETRY)
FEMALE CHOICE
MALE BEHAVIOUR
(TRAIN DISPLAY)
MALE SEX DRIVE
SELECTION PRESSURE

Figure 7