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Tumbler Pigeons Have Smaller Brains

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ABSTRACT

The difference in cerebral or cerebellar structure of pigeon brains can produce the tumbling behavior. Therefore, the aim of this study was to investigate the effects of brain morphology on tumbling behavior in pigeons. To exclude the breed effect as far as possible, in addition to the tumbler pigeons Baska and Homing pigeons were used as controls in the study (4 female and 4 male adult pigeons). Body measurements (BM), live weight (LW), organ weights and histomorphological brain measurements were recorded. The pigeon breeds differed significantly in terms of body and organ morphology. The allometric relationship between brain weight and live weight was significant (P=0.0028). The most values of the Takla birds were below the regression line. This indicates, that the Takla breed has a relatively small brain compared to their body size. The thickness of molecular layer, granular layer and white matter of the cerebellum did not differ between the breeds ($P \geq 0.201$). While the number of Purkinje cells per mm^2 in Baska birds was lower than other breeds, no significant difference was found between Homing and Takla birds ($P \leq 0.05$). No qualitative difference was found in the cerebellar segments of the breeds. In conclusion, the tumbler pigeons have a smaller brain, but they do not differ from other pigeons in terms of general brain histology.

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Introduction

The impact of natural selection on domesticated species has been significantly reduced in favor of artificial selection. While artificial selection gives priority to performance-related traits in livestock species, aesthetic concerns seem to be at the forefront of hobby breeding (Savaş et al., 2007). However, selection based on one or more traits, which ignores the animals' biology and environmental requirements, has led to an increase in reproductive, neurodevelopmental, and behavioral problems in some species (Pajor et al., 2000). For example, in crested ducks, the crest has been reported to cause high levels of malformations in the skull and brain anatomy in embryonal and post-hatch periods, and increased mortality (Portmann, 2000). Cnotka et al. (2008a) reported that crested ducks with a large amount of adipose tissue in the brain showed more motor dysregulation. The authors reported, apart from adipose tissue, these ducks have a smaller brain volume than crested ducks, and found that the cerebellum, apical hyperpallium, tegmentum, and olfactory bulb were significantly smaller in crested ducks than non-crested ducks (Cnotka et al., 2008a).

Domestic animals exhibit greater morphological, anatomical, and physiological variation than their wild ancestors (Kruska, 1988; Cnotka et al., 2008b). Some changes in the selection of some traits, such as body size, color, and behavior, have also led to changes in brain size and composition (Cnotka et al., 2008b). Kruska (1980) reports a dramatic reduction in brain size in domesticated species such as turkeys, rabbits, pigs, sheep, llamas, cats, and dogs. In this context, the large neuroanatomical variation between domesticated species and their origins is attributed to the process of artificial selection as a result of domestication.

The pigeon is one of the oldest domesticated bird species and has a very special place in cultural history (Haag-Wackernagel, 1998). The domestic pigeon is morphologically and physiologically very different from its wild ancestor. Presumably, this variation played an important role in the spread of pigeon fanciers hobby. It is reported that there are about 800 breeds of pigeons, bred mainly for hobby purposes (Vogel et al., 1998). Behaviors are attempted to be explained in terms of the component's movement, adaptation, reproduction, perception, and hormonal mechanisms related to brain activity and morphology (Zeigler and Bischof, 1993). For example, there is a general relationship between cognitive ability and brain weight in mammals and birds (Cnotka et al., 2008b).

The dorsomedial hippocampus and olfactory bulb have been reported to be larger in the functionally adapted brains of homing pigeons, known for their navigational abilities, compared to other pigeon breeds (Mehlhorn et al., 2010). The authors reported that when considering the functional development of the right and left hemispheres in pigeons with navigation experience, the left mesopallium is smaller than the right, while the left mesopallium is larger in pigeons without experience.

The tumbler pigeon exhibits behavior not observed in the wild ancestor. In pigeons, a tumbling behavior consists of the animal rotating backwards around the wing axis during its flight. Nicolai (1976) attributes some diving and related behaviors to genetic mutations and views these behaviors as hypertrophied courtship flight. The wild-type gene versus somersault behavior gene has been reported to have an autosomal incomplete dominant inheritance mechanism; but some differences in the demonstration of somersaults and related behaviors are determined by additional genes (Entrikin and Erway, 1972). Although some tumbling behavior is similar to the motor disorders seen in some mammals, it is not sufficient to describe this behavior as a locomotor disorder caused by a pathology of the inner ear balance mechanism. Because it has been reported that the behavior to likely occur as a result of cerebellar activity (Mowrer, 1940). It is also adding to the reports that the behavior could be due to sensory dysfunction or a change in the feedback mechanism in the central nervous system (Entrikin and Bryant, 1974). Smith et al. (1987) state that the tumbling behavior may have evolved in response to the serotonin mechanism. The authors reported that the behavior may be triggered by general or specific impairment of the spinal cord or higher center of motion.

It is believed that the tumbling behavior may be caused by the differences in the cerebral or cerebellar structure of the pigeons. The aim of the study is to investigate the effects of brain morphology on tumbling behavior in pigeons.

Material and Methods

To rule out the breed effect as much as possible, in addition to tumbler pigeons, two other breeds (Baska and Homing) were used as controls in the study. From each breed there were 4 female and 4 male adult pigeons available. The Takla Pigeon is a breed native to Southeast Anatolia. The Takla pigeons approach their loft with a nosedive, just before landing they roll over and then climb back up perpendicular to the ground and fly on. Baska, with medium length beak, and white flights and head is an exhibition breed, bred specifically in and around Istanbul. Homing pigeons are bred for their long-distance competition all over the world. The body measurements (BM) and live weights (LW) were taken before the dissection of the pigeons. The details of the BM measured with the digital caliper are given in Figure 1.

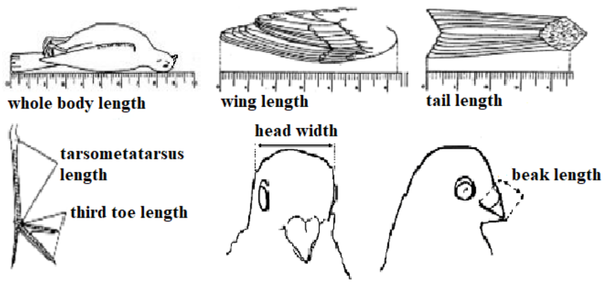

Figure 1. Measurement locations of pigeon body (Baran and Yılmaz, 1984; Savaş et al., 2008)

To study brain histomorphology, the pigeons were euthanized with diethyl ether under anesthesia. In order to preserve the pigeon brains intact, the elements of the occipital condyle that connect the skull to the body were fractured and the brains were completely removed by opening the midline. After measuring the weights of the brains, the tissues were fixed in 4% buffered formaldehyde for 12 hours. Simultaneously the heart and gizzard weights and carcass weights were measured. After fixation, the cerebellums were removed from the hardened tissue and the net brain weights (right and left cerebrum) were measured. To remove the fixative from the tissues, the tissue samples were washed under running water for 10 minutes. Thereafter, the tissues were preserved in 70% ethanol. The dehydration process was performed by running the brain tissue through increasing alcohol series (70, 80, 96%, and finally absolute alcohol). For the translucency process, the tissues were placed in the intermediate medium, xylene, and then were kept in xylene-paraffin (1:1) overnight to acclimate to the paraffin, the embedding medium (Luna, 1968). Optic lobes were removed from the cerebrum immediately before embedding the tissues in paraffin. Thus, three different tissue samples were obtained as cerebrum, cerebellum, and optic nerve lobes. From these tissues, the cerebrum was divided into 3 slices as axial sections 4 mm thick and embedded in paraffin blocks with their occipital lobes facing up. The cerebellums were placed whole in paraffin blocks with the spinal cord forward. The optic lobes are also completely embedded in paraffin blocks. Five micron-thick sections from paraffin blocks were cut on a microtome and stained with hematoxylin and eosin for histomorphological measurements.

The obtained cerebrum and cerebellum tissue preparations were examined under a microscope to examine cerebral and cerebellar differences between the pigeon breeds. Photographs taken of each tissue sample at the same magnification (X4 and X10) were used to schematize them. The thickness of the cerebellar layers was measured using the DP2-BSW program and photographed using a digital camera fitted to an Olympus BX51 model light microscope. The number of Purkinje cells was calculated as the number of Purkinje cells per unit area in the Purkinje layer of the cerebellar sheet.

Statistical Analysis

Data on live weight, organ weights and carcass weights as well as body measurements were analyzed using factorial analysis of variance considering genotype, gender, and interactions. In the analysis of organ weights and carcass weights as well as body measurements, live weight was included in the model as a covariate (SAS, 2002). The Tukey test was used for *post hoc* comparisons.

The relationship between brain weight (BW) and live weight (LW) has been attempted to be explained by the allometry function. The allometry equation was converted to a linear regression equation by taking the logarithm of the dependent and independent variables.

$$y = a \cdot x^b \qquad \log y = a + b \cdot \log x$$

Where y is the independent variable (BW), x is the dependent variable (LW), a is the regression constant, and b is the regression coefficient. If the "b value" is greater than 1, it means the organism is showing positive allometric growth, and if the "b value" is equal to 1, it means the organism is showing isometric growth. The differences between the regression coefficients of the individual allometry functions by breed were tested with contrast in GLM. Because there were no significant differences between the regression coefficients of each breed, a regression plot representing the three breeds was constructed.

Results

The results of the statistical analysis regarding the change of BA by genotype are shown in Table 1. Accordingly, the Baska breed has a shorter body length than other breeds ($P \leq 0.05$). There was no significant difference between the Takla and Homing breeds with respect to this trait ($P > 0.05$). The lowest average wing length was observed in Baska birds, while the highest was observed in Takla birds ($P \leq 0.05$); Homings' wing length was in between these two breeds. While the Takla had the highest mean tail length and the Homing the lowest ($P \leq 0.05$), the Baska was similar to both genotypes ($P > 0.05$). A significant difference was observed for tarsometatarsal length, third toe length, beak length and head width ($P < 0.001$).

According to Table 2, the differences between the LWs of the breeds are significant and the highest average is assigned to Homing and the lowest to Baska ($P \leq 0.05$). While the carcass weights of the Takla and Baska birds are similar, the Homing birds show a higher value ($P \leq 0.05$). It is an interesting finding that the Takla birds have lower BWs than the Baska and Homing birds ($P \leq 0.05$), although BWs of Baska and Homing are similar ($P > 0.05$). The difference between the Homing and Takla genotypes for heart weight was significant ($P < .0.05$), while the Baska genotype had no significant difference from the other breeds ($P > .0.05$). It was found that genotype had no effect on gizzard and liver weights ($P > 0.05$).

Table 3 shows allometric equations between BW and LW for each breed. It was observed that there was no significant difference between breeds in terms of the slopes of the allometric equations ($P > 0.05$). For this reason, an allometry equation was created across the breeds. Figure 2 shows the regression curve expressing the allometric relationship between BW and LW. It was found that there is a significant allometric relationship between brain weight and live weight ($P = 0.0028$). Most of the values of the Takla birds were below the regression line, while the values of the other breeds were above the regression line. This indicates, that the Takla breed has a relatively small brain compared to their body size.

The effect of breed on the thickness of the molecular layer, granular layer and white matter of the cerebellum were not significant ($P \geq 0.201$), while the effect on the frequency of Purkinje cells per mm^2 is significant ($P = 0.040$) (Table 4). While the number of Purkinje cells per mm^2 in Baska birds was lower than the other breeds, no significant difference was found between Homing and Takla birds ($P \leq 0.05$).

The qualitative examination of the cerebellar segments showed no differences in relation to the breeds (Figure 3).

Table 1. Least square-means ($\bar{x}$), their standard errors (SE) of body measurements by breed

Traits, cm	Baska		Homing		Takla		P
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	
Body	28.16^b	0.76	32.16^a	0.73	31.96^a	0.53	0.003
Wing	21.38^b	0.89	22.51^{ab}	0.86	24.10^a	0.62	0.033
Tail	13.73^{ab}	1.08	12.77^b	1.04	15.96^a	0.75	0.025
Tarsometatarsus	2.41^c	0.10	3.30^a	0.09	2.74^b	0.07	<0.001
Third Toe	2.54^c	0.07	3.21^a	0.06	2.93^b	0.05	<0.001
Beak	1.33^c	0.06	1.85^a	0.06	1.57^b	0.04	<0.001
Head Width,	2.42^a	0.04	2.12^b	0.04	2.05^b	0.03	<0.001

Different superscripts indicate significant differences ($P < 0.05$)

Table 2. Least square-means ($\bar{x}$), their standard errors (SE) of organ weights by breed

Traits, g	Baska		Homing		Takla		P
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	
Live Weight	275.90^c	13.47	390.90^a	13.47	339.20^b	13.47	<0.001
Carcass	214.60^b	7.19	252.20^a	6.95	229.50^b	5.00	0.019
Brain	1.84^a	0.06	1.86^a	0.05	1.65^b	0.04	0.003
Heart	3.80^{ab}	0.26	4.56^a	0.25	3.59^b	0.18	0.014
Gizzard	8.86	0.59	9.58	0.57	9.99	0.41	0.274
Liver	6.95	0.63	6.83	0.60	7.54	0.43	0.483

Different superscripts indicate significant differences ($P < 0.05$)

Table 3. Allometric equations between brain weight (y) and live weight (x) by breed

Breeds	Equations	P
Baska	$y = -4.24 + 0.84x$	
Homing	$y = -0.99 + 0.28x$	0.2513
Takla	$y = -4.60 + 0.88x$	

Table 4. Least square-means and their standard errors (SH) of cerebellar traits by breed

Traits	Baska		Homing		Takla		P
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	
PCF/mm^2	8.50^b	0.27	9.50^a	0.27	9.40^a	0.29	0.040
Molecular Layer, um	195.40	17.73	199.60	17.79	240.30	19.15	0.201
Granular Layer, um	405.90	43.02	347.00	43.02	348.14	46.48	0.560
White Matter, um	100.60	12.42	116.00	12.42	94.40	13.42	0.486

PCF: Purkinje Cell Frequency; Different superscripts indicate significant differences (P<0.05)

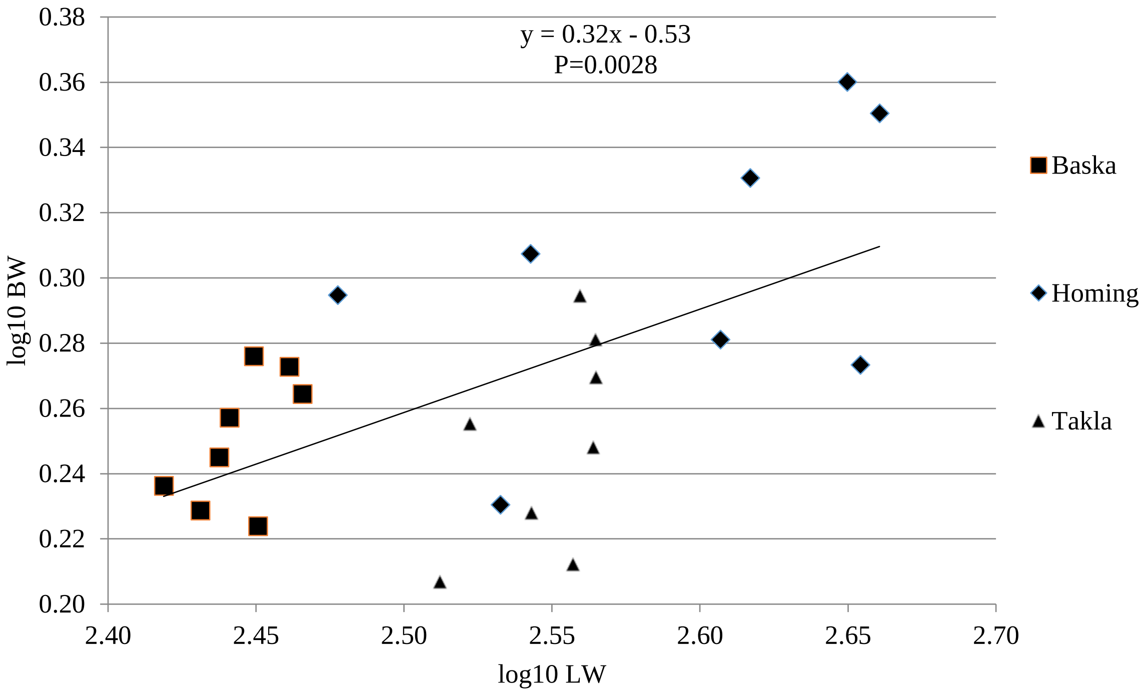

Figure 2. Allometric relationships between brain weight (BW) and live weight (LW)

Discussion

In order to avoid a possible bias that might result from a possible difference in brain histomorphology based on genotype, the Homing pigeons with their high navigational ability (Walcott, 1996) and the Baska pigeons bred for exhibition purposes (Savaş et al., 2008), both non-tumbler breeds, used as comparison birds. The results that the considered pigeon breeds were significantly different from each other in terms of both body and organ morphology showed that suitable pigeon genotypes were selected for comparison with the Takla breed (Tables 1 and 2).

The results showed that the average brain weight of Takla pigeons was about 10% lower than that of the other two breeds. The brain volume of pigeons could not be measured in the study. However, due to the high correlation between brain weight and brain volume reported for birds by Iwaniuk and Nelson (2002), studies on measuring brain volume could be used in the discussion. In a study conducted on barn swallows (*Hirundo rustica*), Møller (2010) states that the variation in head volume is 10.46% in males and 12.16% in females. The brain weight variation found for pigeons in this study was 10.5%. White-crowned sparrow (*Zonotrichia leucophrys*) subspecies that differ on the basis of behavioral ecology (migratory and nonmigratory) can differ by up to 17% in body weight-adjusted brain volume (Vladimir et al., 2007). In a study performed on mice, it was reported that individuals with higher brain weights were more active and exhibited more stereotyped behavior in the maze test (Salimov et al., 2004). However, a direct comparison of the results of our study with these reports is not possible. Because while behavioral changes that occurred in evolutionary processes led to an increase in brain volume (and vice versa), in our study we are dealing with animals that show behavior that can be classified as abnormal for the species. However, the results obtained by comparing tottering mice with normal mice are directly comparable to this study. The cerebellum of tottering mice, used as a model for epilepsy and having motor disorders, is lighter than normal mice (Sawada et al., 2009).

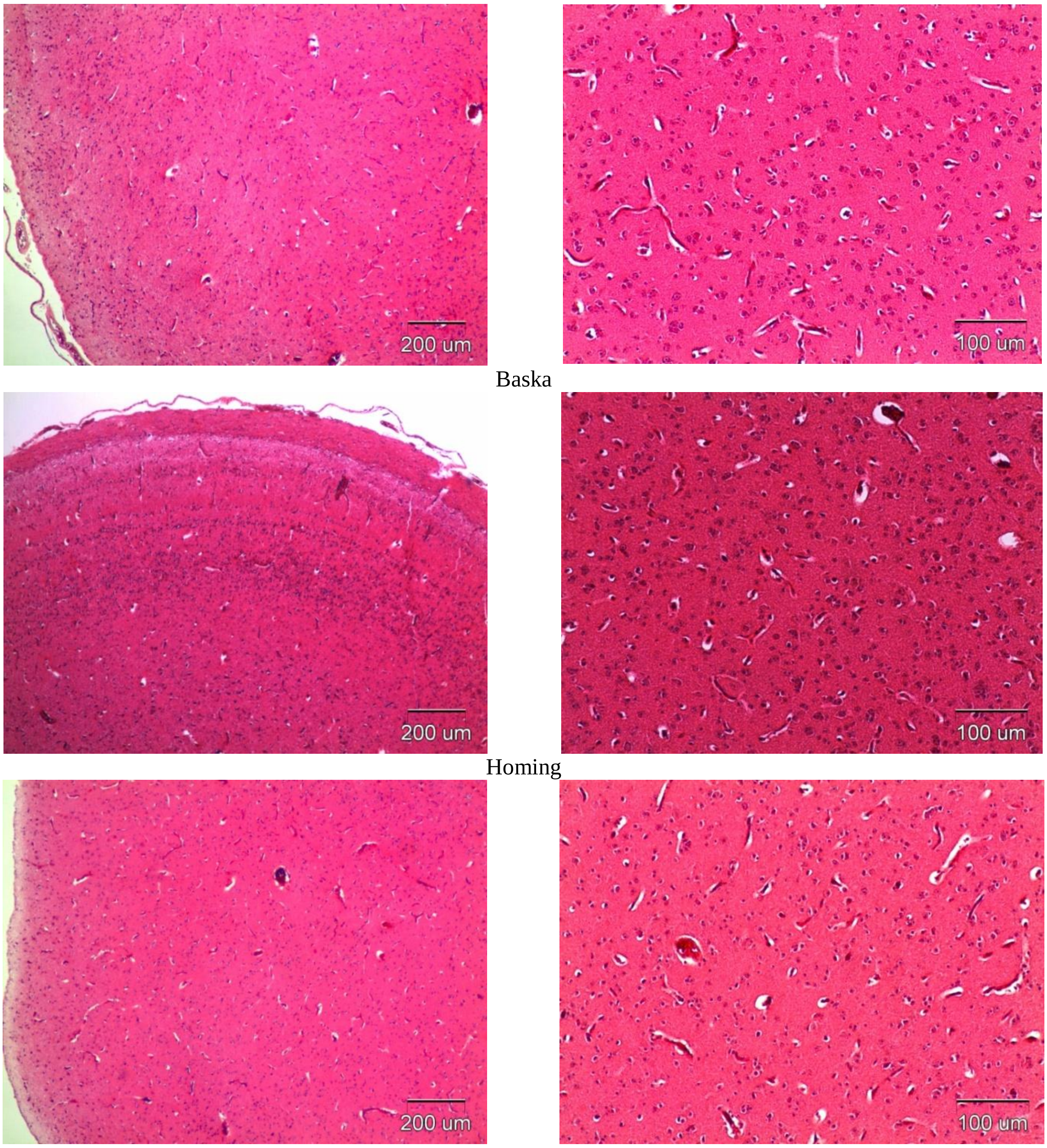

Figure 3. Cerebral cortex and medulla tissue sections of the pigeon breeds

On the other hand, it has been reported that brain atrophy occurs in genetic diseases that cause motor disorders for various reasons, such as: myotonic dystrophy, myotonic myopathy, Huntington's disease (Kassubek et al., 2003; Zhang et al., 2010). It is also known that in Alzheimer's disease, which is known to have a strong genetic origin and causes neurological disorders with age, the brain shrinks faster than in normal elderly people (Spulber et al., 2010).

Møller (2010) reported a 4.5% larger head volume in barn swallows (*Hirundo rustica*) in males than in females. The same rate varies between 12% and 18% in different orangutan subspecies (*Pongo pygmaeus*) (Taylor and Schaik, 2007). In humans, males have larger brains than females (Ricard et al., 2010). Similarly, Miller and Penke (2007) indicate a 10% higher brain weight for men than for women.

The regression coefficients between the estimated live weight and the brain weight of the breeds differed significantly from each other. Accordingly, brain weight increases with body size in all breeds. From the separate or pooled allometric equations of the breeds, it can be seen that brain weight increases relatively slowly compared to weight, indicating a negative allometric relationship. Herre and Röhrs (1973) reported that the b-coefficients obtained from intraspecies brain allometry in domesticated species also show a negative allometry. The slope (b) values compiled by the authors from various studies ranged from 0.166 to 0.300. In a study conducted with geese, it was reported that the same values varied between 0.391 and 0.239 for different breeds (Löhmer and Ebinger, 1982).

Purkinje cells form the outlets in the cerebellum (Sultan and Glickstein, 2007). In this study, when comparing the genotypes in terms of Purkinje density, it was observed that the Baska breed had a significantly lower density than the other two breeds (Table 4). For example, although a decrease in Purkinje cells was observed in tottered mice, this cannot be related to the low density of Purkinje cells in Baska pigeons in this study. Because there is no behavior that can be defined as an anomaly in Baska pigeons. One of the key characteristics that distinguishes Baska birds from Homing and Takla is their lower flight performance. This raises the question of whether there is a possible connection between the functions of Purkinje cells for motor activation (particularly arm muscle kinematics) (Pasalar et al., 2006). The difference between Baska and the other two breeds is that they were bred primarily for their color and appearance, which can potentially negatively impact their ability to fly and navigate. However, it should be noted that these findings are insufficient to directly link Purkinje cells to navigation performance.

Conclusion

The hereditary tumbling and dependent behaviors observed in domestic pigeons are “anomalies” that occur to varying degrees and can have a negative impact on the overall welfare of the pigeons, especially with increasing age. In the results of this study, although tumbling pigeons have a smaller brain, there was no evidence distinguishing Takla pigeons from other pigeons in terms of general brain histology. Tumbling behavior are known to develop with increased age. In this respect, a comparison of young birds with older birds can lead to a clearer finding regarding brain atrophy. In addition, a study of the relationship of the severity of the tumbling and related behaviors seen in a pigeon and its brain histomorphology may be useful in revealing the physiological mechanism of tumbling behavior. In addition, a detailed examination of the brain using immunohistological methods will contribute to the information gathering within the framework of the hypothesis of this study.

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