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Background

In recent years, several Black-throated Thrushes *Turdus atrogularis*, well documented with photographs in Finland and various locations across Europe, have exhibited characteristics not previously considered to occur within the species' known variation. These anomalous features are presumed to result from genetic influence from other taxa, such as the Red-throated Thrush *Turdus ruficollis* and Naumann's Thrush *Turdus naumanni* (Cramp *et al.* 1977, Clement 1999, Clement *et al.* 2000, Duivendijk 2011, Stoddart 2017, Shirihai *et al.* 2018, Collar 2020). The presence of a reddish hue to the tail feathers, notably, has been

deemed an atypical trait for a pure Black-throated Thrush.

Some individuals have displayed a subtle reddish hue on the head, chest, flanks, under and upper-tail coverts, as well as on the wing feathers. Additionally, distinctive characteristics, such as a prominent white supercilium on an individual otherwise consistent with a Black-throated Thrush, or large dark areas and reddish spots on the flanks, are conjectured to signify genetic influence from a Naumann's Thrush or Dusky Thrush *Turdus eunomus* (refer to Photos 1-5).

Drawing from museum materials, the Rarities Committee of BirdLife Finland has assessed these hybrid features in Black-throated Thrushes and



Photo 1: A first-winter male with the outer tail feathers exhibiting a pronounced reddish-brown hue (classified as CD, see the text for the explanations of these codes), the undertail coverts displaying irregular but notably intense reddish colouring, and the flanks showing streaking with a reddish-brown tint. Additionally, a discernible reddish hue is apparent on the bird's head, neck, and wing. Based on these characteristics, this individual was classified as a hybrid between Black-throated Thrush and Red-throated/Naumann's/Dusky Thrush, leading to its publication as such. Joensuu, Finland, 13th February 2013. © Matti Koivula.



Photo 2: A first-winter young female with a notably vibrant red colour in virtually all tail feathers, with the outer ones displaying an almost uniformly reddish tone extending to the base of the feathers (classified as D). The narrowness of the reddish colour in the tail separates it from pure Red-throated Thrushes. Moreover, the bird exhibits a reddish tint on the breast, flanks, and under-tail coverts, and the inner webs of the wing feathers show an orange-reddish colour. This individual was published as a hybrid between Black-throated Thrush and Red-throated/Naumann's/Dusky Thrush. Hamina, Finland, 31st January 2015. © Ari Seppä.

reviewed the Finnish records of Black-throated Thrushes taking this new information into account. This article explains the principal findings of our research, offering insights that may be applicable to the evaluation of observations in other European countries.

Taxonomy and geographical distribution

In modern taxonomy, Black-throated Thrush is considered a monotypic species (Collar 2020). In the past, it was grouped with Red-throated Thrush (Clement 1999, Clement *et al.* 2000); however, based

on the taxonomic recommendations for British birds (Knox *et al.* 2008), the British Ornithologists' Union Records Committee (BOURC) in 2009 and the Taxonomic Committee of the European Rarities Committees (AERC TAC) in 2010, they were designated as separate species (BOURC 2009, Crochet *et al.* 2010). The same decision has been adopted also in the widely used International Ornithological Committee's (IOC) World Bird List (Gill *et al.* 2024).

The decision to classify these taxa as separate species has faced criticism, primarily due to the limited differences in plumage characteristics and vocalisations (Arkhipov *et al.* 2003, Knox *et al.* 2008, Shirihai *et al.* 2018). This becomes particularly



Photos 3a and 3b: While this first-winter bird exhibits some features consistent with a Black-throated Thrush, it is still a clear hybrid (classified as CD) based on its reddish-brown tail feathers. Notably, the white area of the throat extends further down to the breast than is typically observed in Black-throated Thrush, and the inner webs of the wing feathers display widespread reddish-brown, wedge-shaped patterns. Another characteristic inconsistent with a Black-throated Thrush is the presence of a very wide, extensive, and white supercilium. Although most of the features deviating from typical Black-throated Thrush characteristics align well with those of Naumann's/Dusky Thrush, the possibility of Red-throated Thrush genetic influence could not be entirely ruled out. Consequently, this individual was published as a hybrid between Black-throated Thrush and Red-throated/Naumann's/Dusky Thrush. Kajaani, Finland, 22nd February 2017. © Jouni Ruuskanen.



Photo 4a and 4b: This individual might initially be mistaken for a pure first-winter Black-throated Thrush, but the distinctive markings associated with other thrush species become evident when the bird fans its tail (classified as D) and spreads its wings. Although the reddish tones on the bird's head and particularly the widely reddish-brown tail feathers, could be indicative of a Red-throated Thrush, the diverse reddish pattern on the underparts and especially on the flanks still distinctly points to the influence of Naumann's/Dusky Thrush. Additionally, the prominent orange-reddish areas on the rump, wing feathers, and greater upper-wing coverts led to the classification of this individual as a hybrid between Black-throated Thrush and Red-throated/Naumann's/Dusky Thrush. Helsinki, Finland, 12th February 2017. © Petteri Hytönen.



Photos 5a and 5b: This bird was found dead, which enables a detailed examination. The tips of the bird's tail feathers display distinct reddish wedge-like patterns (classified as C), with the same hue in places extending towards the base of the tail-feathers. Notably, the flanks, vent, and under-tail coverts exhibit extensive orange-red spot-like areas, and clear orange regions are also evident on the inner webs of the primaries. These characteristics point to the influence of Naumann's/Dusky Thrush genes. However, given the potential genetic contribution from Red-throated Thrush, this individual was designated as a hybrid between Black-throated Thrush and Red-throated/Naumann's/Dusky Thrush. Inari, Finland, 10th December 2019. © Aleksi Lehikoinen, Helsinki, Finland (The Finnish Museum of Natural History).

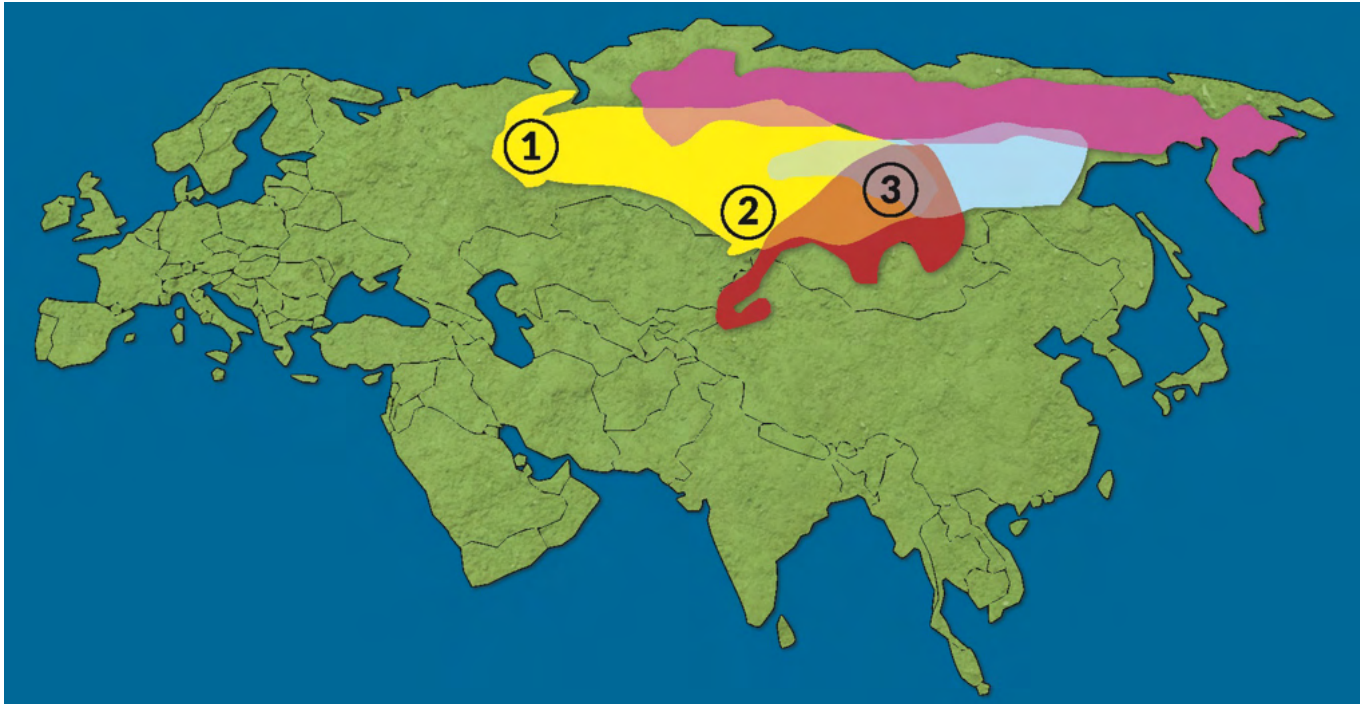


Figure 1: The breeding ranges of Black-throated Thrush (depicted in yellow) and its eastern counterpart species, namely Red-throated (in red), Naumann's (in light blue), and Dusky Thrush (in purple), show substantial overlap. In these intergradation zones, a significant proportion of birds are known to display varying degrees of hybrid characteristics. To assess the variation in plumage characteristics of Black-throated Thrush as it transitions towards red-tailed thrush taxa, museum specimens were divided into three groups, originating from three regions of the breeding distribution area: (1) western, (2) central, and (3) eastern. The depicted ranges are based on BirdLife International maps. © Seppo Alanko, originally published in Huhtinen et al. 2020.

problematic considering the well-documented extensive cross-breeding between Black-throated, Red-throated, Naumann's, and Dusky Thrushes, within their contact zones (McCarthy 2006). Various kinds of hybrids are frequently encountered in the wintering areas too (Clement 1999, Clement *et al.* 2000, Wassink *et al.* 2007).

The interbreeding of closely related taxa may extend beyond the first generation, potentially involving re-crossing or gene flow from another species over several generations (Ottenburghs *et al.* 2017). Leonid Portenko, who extensively studied thrushes and their hybrids in Russia, proposed considering all four taxa as subspecies of the polytypic *Turdus ruficollis* (Portenko 1981).

Within the northern boreal zone, Black-throated Thrush breeds from the European slopes of the Ural Mountains to Transbaikali in central Siberia (Shirihai *et al.* 2018, Collar 2020). It shares breeding areas particularly with Red-throated and Naumann's Thrushes (Figure 1). In the northern regions, the

breeding range of Black-throated Thrush intersects with that of Dusky Thrush. These birds migrate to the Middle East, the Himalayas, and southern China, and as far as northern Myanmar.

In Finland, Black-throated Thrush is predominantly a vagrant in late autumn, coinciding with other thrush movements. Several individuals have been noted to overwinter at the same location well into spring (Väisänen *et al.* 2020, Huhtinen *et al.* 2020). Apart from autumn and spring migration observations, a few noteworthy occurrences have been documented in late spring and summer.

Tail colouration

Using museum specimens, BirdLife Finland's Rarities Committee undertook an examination of the plumage characteristics of Black-throated Thrush, with a specific focus on tail feather patterns and, more broadly, the prevalence of red colouration in the tail



Photo 6: Black-throated Thrush - type birds were categorised according to tail colouration and patterns (from top to bottom): (A) entirely dark-tailed, (B) subtle reddish hue, (C) reddish wedge-shaped patterns, (D) extensively reddish outer tail feathers, and (E) strikingly red tail feathers. © Hannu Huhtinen and Aleksi Lehikoinen, St. Petersburg, Russia (Zoological Museum of the Zoological Institute of the Russian Academy of Sciences).

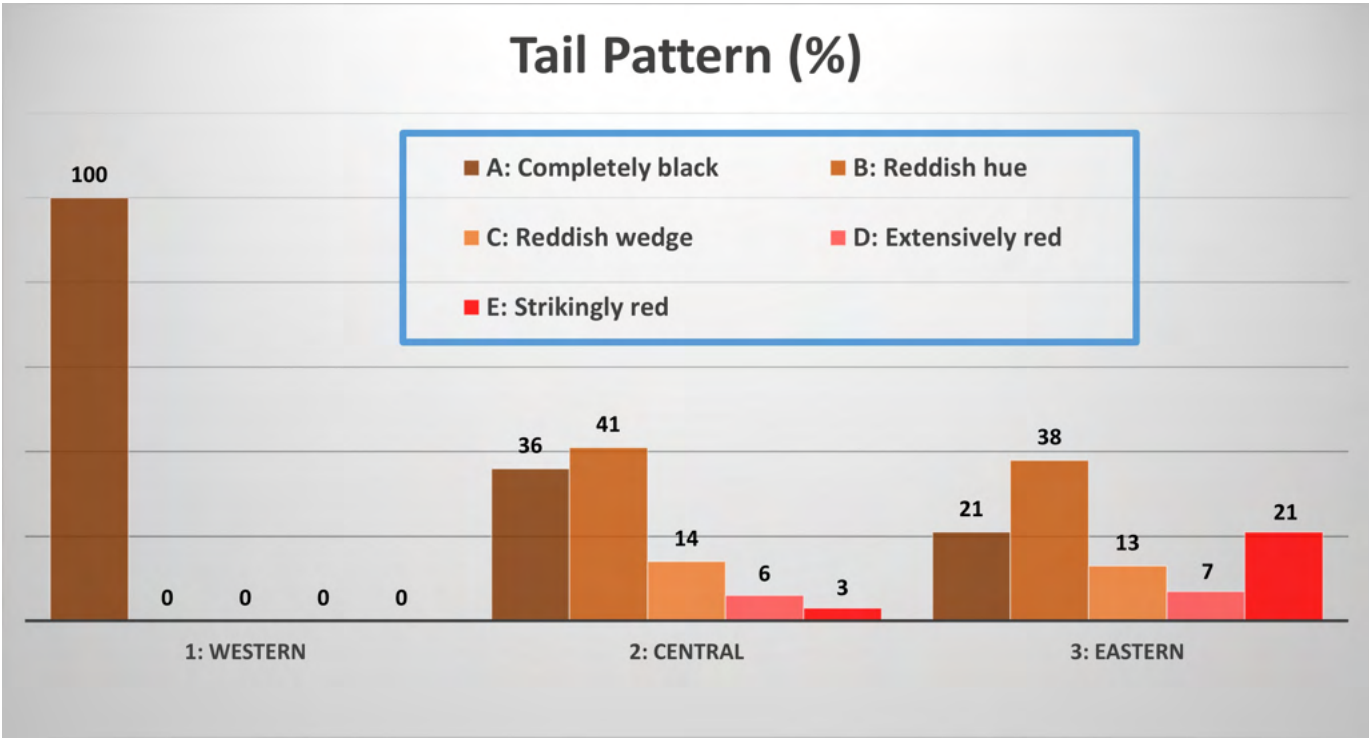


Figure 2: Using skin specimens from museums, the percentages of the tail colour classes in Black-throated Thrushes and individuals closely resembling these, were calculated across three geographical areas. The specimens were collected from the breeding grounds of during the nesting period. The sample includes 21 individuals from the western region, 164 from the central region, and 49 from the eastern region. The prevalence of red in the tail, as well as the proportion of individuals with red tails, show an increasing trend as one moves eastward.

feathers across its geographical range, from the western breeding areas eastward towards regions inhabited by red-tailed species. The primary challenge lay in the restricted number of thrush samples from the breeding grounds available in Western European museums. Birds collected from the wintering areas were excluded from the study due to the lack of precise information about their specific breeding grounds.

A comprehensive number of individuals from the breeding grounds was studied in the Zoological Museum of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, and the Zoological Museum of M. V. Lomonosov Moscow State University, Moscow, Russia, categorised into three geographical zones in the west-east direction (refer to Figure 1):

1. The westernmost breeding grounds of Black-throated Thrush, situated as distant as possible from other closely related red-tailed thrush taxa (Ural Mountains, Komi Republic, Arkhangelsk).
2. Central breeding grounds (Krasnoyarsk Region, Altai Republic).
3. The easternmost breeding areas of Black-throated Thrush, where distribution notably overlaps with

species like Red-throated and Naumann's Thrush (Irkutsk Oblast, Buryatia, Transbaikali).

As the tail features are easiest to categorise, specimens were classified into five categories based on the colouration and patterns of the tail feathers (Photo 6):

- A. Completely black or grey/dark-brown tail feathers without a reddish hue.
- B. A subtle reddish hue, particularly on the outer tail feathers.
- C. Reddish, distinct, and typically wedge-shaped pale/reddish patterns on the tips of the outer tail feathers.
- D. Extensively reddish outer tail feathers, with the reddish colour extending up to the base of the tail and also visible on a closed tail.
- E. Strikingly red tail feathers, indistinguishable from red-tailed thrush taxa based on the tail feather characteristics.

This study encompassed all age groups and both sexes. Analysis of the skin collection data revealed that in the Urals the individuals were exclusively dark-

tailed, while less than half of the individuals were black-tailed on the central breeding grounds, with less than a quarter on the eastern breeding grounds (Figure 2). The findings indicate that pure Black-throated Thrushes lack red in the tail, and that the influence of red-tailed thrush taxa - Red-throated Thrush and Naumann's Thrush - on the Black-throated Thrush genome appears to intensify in areas of range convergence or overlap. Given that pure Dusky Thrushes, akin to pure Black-throated Thrushes, possess an entirely black tail, tail classification alone cannot differentiate between the hybrids of these species, making it necessary to consider other hybrid features.

Assessment of other hybrid traits

The literature pertaining to Asian thrush species has addressed Black-throated Thrush and the interbreeding of closely related thrush species (Portenko 1981, Clement 1999, Clement *et al.* 2000, McCarthy 2006, Shirihi *et al.* 2018, Collar 2020). For instance, the museum collections of St. Petersburg had been organised into pure Black-throated Thrushes and various crosses based on the characteristics outlined in the studies. Seven characteristics were identified as pivotal for assessing hybrid origin. The hybrid traits manifest themselves in the plumages as follows, and comparison of the extremes of the hybrid features are given in Photos 7 - 11:

1. Colour of the vent, under-tail coverts, and flanks.
2. Breast colour.
3. Colour of the head and neck sides.
4. Distinctness of the supercilium.
5. Colour of the remiges.
6. Colour of the greater upper-wing coverts.
7. Shape of breast and flank patterns: streaks/spots.

Each plumage feature was assessed on a six-step scale to find characteristics inconsistent with a Black-throated Thrush. The cumulative assessment of all characteristics provided an indication of whether the Black-throated Thrush exhibited traits suggestive of other thrush species (negative) or if the overall profile was more aligned with the Black-throated Thrush (positive). The scoring for different plumage areas was as follows:

- +1: Based on the photographs, it was apparent that the feature aligns with a typical Black-throated Thrush.
- +0.5: Based on the photographs, it could be inferred

that the bird lacked distinct hybrid traits, although minor deviations were not conclusively discernible.

0: The plumage character was not distinguishable from photographs.

-0.5: The characteristic mildly implied another species, but the trait was faint, or conversely, uncertainty existed regarding whether the negative trait was merely an illusion due to photo quality.

-1: Clearly an unsuitable trait for a Black-throated Thrush, though the trait was not markedly pronounced.

-2: A feature significantly incompatible with a Black-throated Thrush.

Classification of the Finnish Black-throated Thrush observations

The objective of the classification was to establish criteria for birds that can be officially published as Black-throated Thrush. Additionally, the classification seeks to raise awareness among birdwatchers regarding the challenges in identifying eastern thrush species, as well as showing the need for meticulously documenting the plumage characteristics.

The initial step involved distinguishing observations with insufficient descriptions for assessment, and the exclusion of sightings likely associated with a thrush taxon other than the Black-throated Thrush.

Subsequently, observations were categorised based on tail characteristics into classes A, B, C, D, and E, if it was determined that the tail patterning aligned with only one class, or, if not, a combination of the classes. An additional class F was introduced for instances where tail estimation from photographs or written descriptions lacked reliability. Older observations, particularly those reliant on written descriptions or with poor-quality photographic documentation, were placed in this category. Credibility issues arose with written descriptions where the bird's tail was noted as black or non-red, despite photographs depicting a distinct red hue.

Scores for other hybrid traits or minor deviations were assigned based on photographs, and a cumulative score was computed for each observation. Ultimately, these two sub-assessments were combined to form an overall evaluation, determining the acceptance category of the observation. The overall assessment placed findings into the following categories:

Black-throated Thrush *Turdus atrogularis*:

Class 1 (A, AB, ABC). Classical Black-throated Thrush, including individuals with minor abbreviations that



Photo 7: The base colour on the flanks of the upper Black-throated Thrush is white, and the streaking on the flanks is distinctly grey. The vent and under-tail coverts are completely white and lack any reddish-brown hues. In contrast, the individual with hybrid features at the bottom displays a broader brownish colouration on the flanks, with certain feathers exhibiting striking reddish streaks that extend widely towards the edges of the feathers. The primary difference between the individuals lies in the under-tail coverts, which are markedly and widely reddish-brown in the lower individual. © Hannu Huhtinen, Tring (The Natural History Museum at Tring).



Photo 8: The colour of the breast and throat feathers in the pure Black-throated Thrush on the top is distinctly dark grey, with the edges of the feathers being white and devoid of reddish-brown hues. In contrast, the centres to all breast and throat feathers, in the individual with hybrid features on the bottom, exhibit a widespread reddish-brown tint. This pronounced hybrid trait resulted in a -2 score for the assessment of breast colour. © Hannu Huhtinen, Tring (The Natural History Museum at Tring).



Photo 9a and 9b: In the pair of images on the left, the lower individual's head exhibits a distinctly cold grey tone, well-suited for a pure Black-throated Thrush. In contrast, the upper individual displays pronounced reddish-brown hues on the lores, supercilium, ear-coverts, submoustachial stripe and in the eye ring, a clear indication of the influence of Red-throated or Naumann's Thrush. Similarly, in the right-hand image pair, the lower individual shows uniform grey to the sides of the crown, with no indication of a paler supercilium. The broad and white supercilium of the upper individual, extending from the base of the bill to the rear of the ear-coverts, once again points to the influence of Naumann's or Dusky Thrush in the bird's genome. © Hannu Huhtinen, Tring (The Natural History Museum at Tring).

could not be conclusively ruled out.

Class 2 (BC, C). Individuals with observable minor abbreviations inconsistent with the Black-throated Thrush.

Class 3 (F). Individuals where the potential for hybridization could not be entirely excluded.

Hybrids (CD, D, E):

Black-throated Thrush X Red-throated/Naumann's /Dusky Thrush *T. atrogularis* X *T.*

ruficollis/naumanni/eunomus

The cumulative scores for hybrid traits 1 - 7, along with the tail categories and the ultimate acceptance classes, are illustrated in Figure 3. Examples of individuals placed in different acceptance categories are shown in photos 12 - 14. It should be remembered that in many cases there is a relatively high likelihood of a genome effect from more than two parent species. Additionally, acceptance of individuals with deviations under the name Black-throated Thrush does not imply that these traits necessarily belong to the inherent variation of the species. Given the challenges of detecting subtle deviations in field conditions, this pragmatic classification was chosen to streamline the processing of observations and publication criteria.

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Photo 10: The undersides of the primaries in the lower individual are consistently grey, resembling the pure Black-throated Thrush. In contrast, the primaries of the upper individual appear predominantly brown, with translucent reddish areas forming on the inner webs. Such colouring of the wing feathers does not occur in Black-throated or Red-throated Thrush, clearly indicating the influence of Naumann's or Dusky Thrush. © Hannu Huhtinen, Tring (The Natural History Museum at Tring).

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Photos 11a and 11b: The left specimen shows the characteristic grey greater upper-wing coverts of a Black-throated Thrush. Conversely, the reddish-brown wing coverts of the right individual clearly indicate the influence of Naumann's or Dusky Thrush. Similarly, in the right-hand image, the right specimen displays the typical features of a Black-throated Thrush, with the grey streaks on the flanks relatively narrow and centred around the feather shafts. The right individual's flank feathers have broad, dark, wide-spotted centres, providing a clear indication of the influence of Naumann's or Dusky Thrush in the individual's genome. © Hannu Huhtinen, Tring (The Natural History Museum at Tring).

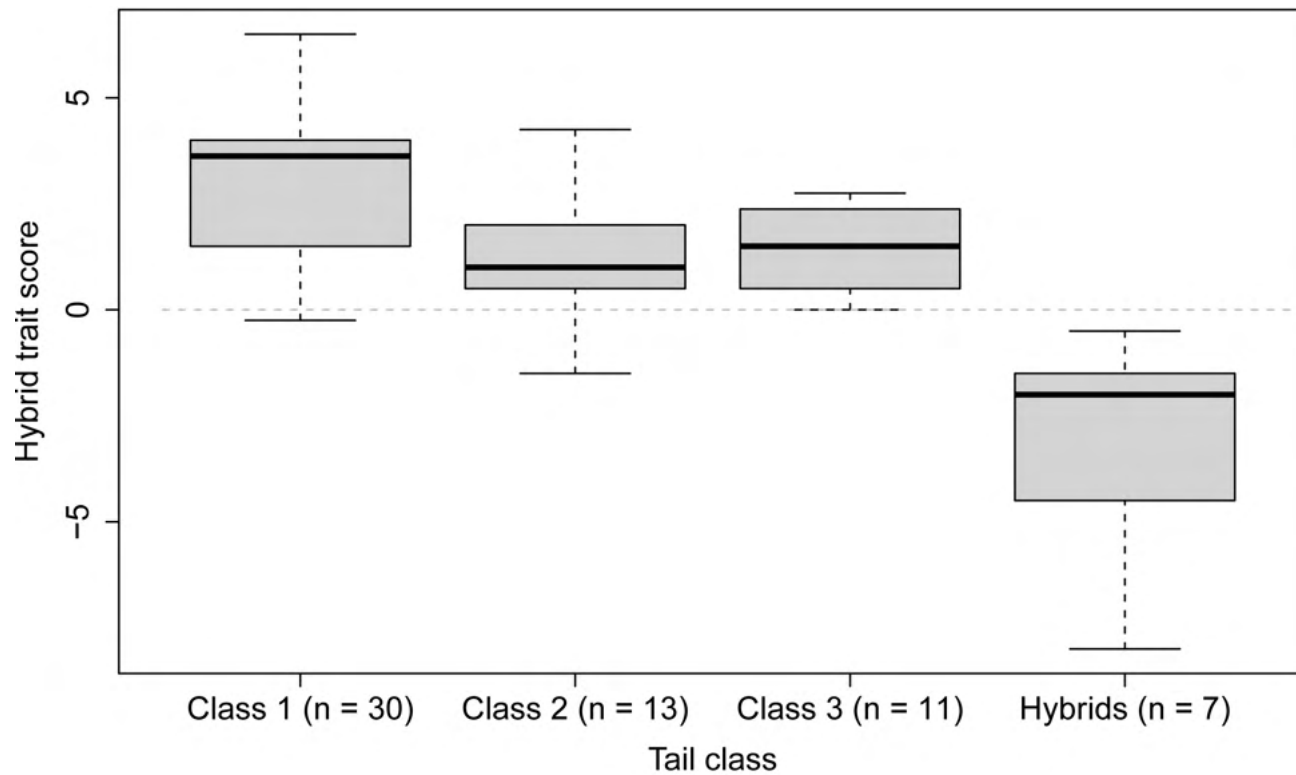


Figure 3: The overall score for hybrid features is presented in relation to tail classification and final acceptance classes in photo-documented specimens (Class 1 = A, AB, ABC; Class 2 = BC, C; Class 3 = F; Hybrids = CD, D, E). Classes derived from tail patterns exhibit a notable correlation with the scoring of hybrid features in other plumage characteristics. Positive values, indicative of a pure Black-throated Thrush, diminish proportionally when the colouring and patterning of the tail shift towards hybridization from class A to class D. Similarly, individuals classified as hybrids based on tails (CD and D) also exhibit distinctly negative values for other features. This supports the accuracy of the delineation between those identified as hybrids and those accepted as Black-throated Thrush, given the level of documentation. Class F comprises birds for which tail colouration is not adequately documented. The proportion of classic 'pure' Black-throated Thrushes is low in the overall material. The boxes represent the quartiles of observations on both sides of the median, and the whiskers depict the extreme values of the class.



Photos 12a and 12b: The reddish-brown patterns observed on the wing feathers of Black-throated Thrush indicate influence of Naumann's or Dusky Thrush in its genome. The extensively reddish base of the tail feathers, as per the illustrated classification, provides substantial grounds for interpreting hybridization. A reddish-brown hue is also evident on the under-tail coverts, in the streaking of the flanks, and on the sides of the neck and head. Furthermore, the edges of the greater upper-wing coverts and tertials exhibit a reddish colour. A hybrid Black-throated Thrush, *Turdus atrogularis* X *T. ruficollis/naumanni/eunomus*. Helsinki, Finland, 27th February 2020. © Petri Pietiläinen.



Photos 13a and 13b: In the field photograph, this individual appears to be a typical adult winter male Black-throated Thrush, exhibiting no reddish-brown hues on its plumage. Additionally, the tail feathers examined in the hand display a uniformly dark, blackish colour without any discernible reddish hue. Upon closer inspection, however, a relatively clear reddish tinge on the under-tail coverts is visible. Nevertheless, according to the established criteria, having only one unsuitable trait is insufficient to decrease the total hybrid trait score, as calculated in the assessment, to the level required for the hybrid category. Therefore, this individual was considered to meet the standards for acceptance in class 1. Espoo, Finland, 15th December 2021. © Jari Laitasalo (left) and 19th January 2021. © Roni Väisänen (right).



Photos 14a and 14b: This adult female Black-throated Thrush exhibits a wedge-shaped pale reddish pattern at the tip of the outermost tail feathers, resulting in the tail being classified as class C. Among other plumage details, only the sides of the head, throat, and breast display a slight reddish hue. Consequently, in the overall assessment, this individual was assigned to acceptance class 2, indicating observable minor abbreviations inconsistent with the typical characteristics of the Black-throated Thrush. Tampere, Finland, 2nd February 2021. © Pekka Suhonen.