"How not to judge a deer by its cover": a personality assessment study on captive adult red deer males (*Cervus elaphus*)

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Abstract

Personality is not a uniquely human characteristic and it has been documented in a wide range of organisms, from mammals to birds, reptiles, fish and invertebrates. However, personality is still poorly understood in Cervids. Therefore, our study aimed to fill this gap by i) investigating personality and ii) exploring its links to dominance hierarchy, assessed by behavioral observations in 11 captive and tame male red deer (*Cervus elaphus*). Using questionnaires to assess personality, three trained volunteers rated these animals in 15 behaviorally composed adjectives with detailed descriptions, based on their overall impression at the end of the observation period. Behavioral data from animals was collected across three different situations, namely "feeding" (i.e., high competition for a scarce resource), "normal" (i.e., no external stimuli) in a group setting, and "handling" (i.e., stressful situation due to human manipulation) in an individual setting. We estimated dominance hierarchies between the individuals based on situations of average and high competition (i.e., "normal" and "feeding") via the Clutton-Brock Index (CBI). Using Fleiss' Kappa for inter-rater reliability, only five of our 15 behavioral adjectives showed acceptable reliability. Using principal component analysis, four of these adjectives formed one personality component labelled "Confidence/Aggressiveness". We found that although "Confidence/Aggressiveness" did not correlate with CBI, ratings of two adjectives loading onto this component, namely "Confident" and "Submissive", significantly correlated with the CBI, indicating that questionnaire ratings reflect real behavioral variation in red deer males. Our study provides the first assessment of personality in male red deer and adds to the growing literature on Cervid personality, offering the basis for future personality research in ungulates.

Keywords: personality assessment, questionnaires, dominance hierarchy, red deer, Cervids

1. Introduction

Animal personality represents one of the most intriguing challenges in behavioral research (Wilson et al. 2019; Weiss 2018) and tends to be described as "between-individual behavioral differences consistent across time and contexts" (Réale et al. 2010; Réale et al. 2007; Sih, Bell, and Johnson 2004). In animal behavior science, these between-individual differences were traditionally considered a "noisy" variation around an adaptive population mean; however, during the last decades, statistical models have developed such that this variation can be quantified (Araya-Ajoy and Dingemanse 2014; Dingemanse and Dochtermann 2013; Dingemanse et al. 2010; Martin et al. 2019). Furthermore, personality has been linked to consistent inter-individual variation in ecologically relevant situations (Réale and Montiglio 2020), for instance foraging (Wilson and McLaughlin 2007), dispersal (Dingemanse and de Goede 2004), acquisition of dominance ranks (Fox et al. 2009), group joining preferences (Harcourt et al. 2009) or cognition (Boogert et al. 2018).

Researchers have identified several important axes of animal personality in which individuals can be placed in a wide range of organisms, from mammals to birds, reptiles, fish and invertebrates (Gosling 2001; Carere and Maestripieri 2013). These axes are usually labelled shyness – boldness, exploration – avoidance, aggressiveness, activity, sociability and proactive – reactive stress coping styles (Bergmuller and Taborsky 2010; Finger et al. 2018; Koolhaas et al. 1999; Réale et al. 2007). Some of these axes, such as boldness-shyness (Dahlbom et al. 2011), aggressiveness (Drent, Verbeek, and Boon 1996; Rodriguez-Santiago et al. 2020) and exploration-avoidance (Verbeek et al. 1999), have been associated with a higher position in the hierarchy or with changes in the dominance status (Rudin, Tomkins, and Simmons 2016). These changes can have repercussions on the behavior or survival of the affected individuals in both natural populations and in captive groups (Rudin, Tomkins, and Simmons 2016).

The general relationship between dominance rank as well as leadership and personality is still poorly understood (Gosling and John 1999; Kurvers et al. 2009); however, an increasing number of studies have demonstrated a link between these attributes in different species. For example, personality traits like exploration or boldness are linked to leadership in several species [barnacle geese (*Branta leucopsis)* (Kurvers et al. 2009), zebra finches (*Taeniopygia guttata*)

(Beauchamp 2000; Schuett and Dall 2009), and three-spined sticklebacks (*Gasterosteus aculeatus*) (Harcourt et al. 2009)] and are linked to dominance rank in some other species [e.g., rainbowfish (M*elanotaenia duboulay*) (Colléter and Brown 2011)]. In Barbary macaques (*Macaca sylvanus*), higher scores in confidence are linked to higher positions in dominance ranks (Konečná et al. 2012). Konečná and colleagues (2012) suggested that these findings lead to testable predictions, such as, for example, that scoring highly in confidence could be associated with higher positions in new troops for immigrating, previously low-ranking, males. High confidence could also help high-ranking animals keep their social positions longer (Konečná et al. 2012). In female rhesus macaques (*Macaca mulatta*), dominance rank is linked to social approachability and boldness (Kohn et al. 2016). However, boldness is not always linked to higher social positions or higher reproductive fitness. In hermit crabs (*Pagurus bernhardus*), the individuals that produce the most offspring are also the most risk-averse (Bridger, Bonner, and Briffa 2015). Personality can shape populations and social groups in different ways, as documented in red deer, where males are not merely dominant or subordinate, and their role in the group cannot be simply described via rank order, i.e., by not taking into account the perception of the interaction and of the rank itself (Esattore et al. 2020).

Despite increasing efforts in the last decades to describe personality in a multitude of species, the literature that investigates the consistency of behavioral patterns in ungulates in general, and Cervids in particular, still only counts a few species (e.g., Bergvall et al. 2011; Jennings, Hayden, and Gammell 2013; Monestier et al. 2016; Found and Clair 2016). These studies focused on the trade-offs between anti-predatory behavior and foraging, pointing out that boldness, but not dominance, was related to time spent foraging in fallow deer (*Dama dama*) (Bergvall et al. 2011). Other studies demonstrated the inter-relationship between aggressiveness, willingness to fight, mating success and fitness in rutting male fallow deer (Jennings, Hayden, and Gammell 2013). Furthermore, some studies looked at the boldness scores of elk (*Cervus elaphus canadensis*) and their link to migration pattern with potential consequences for wildlife population management decisions (Found and Clair 2016) or on the individual variation in acute stress response, focusing on the link between coping mechanisms and individual condition in captive roe deer (*Capreolus capreolus*) (Monestier et al. 2016).

It is interesting to note that red deer (*Cervus elaphus*), a large ungulate species, has not yet been thoroughly explored in terms of its personality, likely due to the elusive nature of this species or logistical issues related to studying them in the wild. Occurring in most continents, either as part of the native fauna or being introduced (Lovari 2018), red deer have experienced an increase in popularity during the last decades, also due to the establishment and development of deer farming across the world (Urošević et al. 2018) and their biology has been intensively investigated in a number of disciplines (for a general overview see Clutton-Brock, Clutton-Brock Guinness, and Albon 1982). However, previous studies on farmed red deer only looked at very specific aspects of behavioral consistency, e.g., in a handling context (aggression towards the handler) or under rather artificial rearing conditions (Schütz et al. 2016; Pollard and Littlejohn 1995). In addition, if, and to which extent, some personality characteristics like boldness or aggressiveness are related to some aspects of red deer male social behavior, for example, their position in the dominance hierarchy, is still unknown. In fact, in red deer, as well as in other polygynous ungulates engaging in a restricted period of sexual activity (Santiago-Moreno et al. 2007; Willisch and Neuhaus 2010), males invest significant energy attempting to gain a high rank, which later ensures that they receive privileged access to resources (i.e., food, mates) (Barroso, Alados, and Boza 2000; Favati, Leimar, and Løvlie 2014).

Thus, in this study we investigated the personality of adult red deer males and its links to the dominance hierarchy, assessed with behavioral observations under captive conditions. Our aim was (i) to discover whether trait ratings evaluated with a newly constructed red deer questionnaire, based on impressions gathered after a period of behavioral observations, fully capture these animals' behavioral variation and (ii) to link deer personality with their dominance rank in bachelor groups. We predicted that the male red deer individuals would consistently differ in their personality traits. Furthermore, we hypothesized that differences in male deer personalities would be linked to their differences in ranks, namely that the bolder and/or more aggressive males would also be higher in rank and vice versa.

2. Materials and Methods

2.1. Study animals and facility

The study was conducted at a deer facility belonging to the Institute of Animal Science (V.Ú.Ž.V), located in Podlesek, Prague, Czech Republic (50°03'02.2"N 14°35'37.1"E). The experimental deer farm is an accredited research facility in accordance with the European and Czech laws for ethical use of animals in research and the experimental proposal n° MZe 1297 was approved by the Animal Care and Use Committee. Tame red deer males (25 in total; 11 adults, 14 juveniles) were kept in three inter-connected enclosures, covering an area of approximately 2 hectares (ha) and housed separately from the females. This housing system is designed to recreate the natural conditions, where animals of different sexes live segregated for most of the year and eventually merge for mating (Mitchell 1977; Clutton-Brock, Clutton-Brock Guinness, and Albon 1982). Each enclosure (of about 0.7 ha) contained a shelter (a wooden, roofed barn, with one longer side permanently open covering an area of approximately 24 m^2), a water reservoir, and a mud pool for wallowing. The animals fed mostly on the pasture and were supplemented with hay (*ad libitum*) and occasionally with a mixture of soy, barley and oats, together with a mineral/vitamin premix which amounted to an average of 0.7 kg/day/animal. Individual deer were identified by colored, numbered collars and all had names. We decided to focus only on adult males of the herd (N=11) that were minimum of five years old, and up to ten years old (median age: 7). Male behavior is suggested to be more repeatable than female behavior for two main reasons: first, due to testosterone levels (Andrew 1972; Wingfield 1994; cf. Bell, Hankison, and Laskowski 2009) and second, due to male behaviors that are under sexual selection, as the predictability of males in certain behavioral traits is often linked to their behavior in another, inter-connected context (Bell, Hankison, and Laskowski 2009; Garamszegi et al. 2006; Kokko 1998). We only studied adult animals (N=11) since, as described in humans (Roberts and DelVecchio 2000), mallards (Butler et al. 2011) and red squirrels (Kelley et al. 2015), personality is shown to go through changes along with development (Class and Brommer 2016; Stamps and Groothuis 2010). In addition, the consistency of behavior increases with maturity (Øverli et al. 2007).

2.2. Personality Assessment

Two different methods are usually used to study personality, sometimes in conjunction, namely behavioral coding and trait rating (Freeman, Gosling, and Schapiro 2011; Šlipogor et al. 2020). Behavioral coding aims to capture the behavioral repertoire of a focal animal in either natural or experimental conditions. In contrast, the method of trait rating requires a team of experienced raters to score a focal animal on a set of multiple behavioral descriptors (Freeman, Gosling, and Schapiro 2011; Koski 2011). To conduct trait rating assessment, we compiled a personality questionnaire, based both on the "bottom-up traits" (Stevenson-Hinde and Zunz 1978; Uher 2008, 2011, 2011), relevant for the species' behavioral repertoire, and the "top-down traits", previously used in other questionnaires on deer (e.g., Bergvall et al. 2011), elephants (Seltmann et al. 2018) and primates (Eckardt et al. 2015; Koski et al. 2017; Weiss 2017). We started with a larger set of items (47 items from Bergvall et al. 2011, 30 items from Lloyd et al. 2007, 30 items from Seltmann et al. 2018, 23 items from Stevenson-Hinde and Zunz 1978). However, since our sample size was limited, we decided that the final questionnaire should not have included more than 15 items. Given that we had to limit our choice of items, we tried to avoid items that represent similar behaviors (e.g., "inquisitive" and "curious" or "submissive" and "timid"). Furthermore, we decided to include items that are relatively straightforward, easy to understand for raters and that the authors had encountered often in personality research. Prior experience with red deer also helped to guide the selection of items for the questionnaire.

Two of the three raters were acquainted with the animals for two months (February-March 2018); the third rater had known the animals for longer, as they had previously been the subject of different studies. Successively, the raters conducted behavioral observations of the animals for four months (April-July 2018). Therefore, all raters were familiar with the target animals and based their ratings both on the behavioral data collected previously and on their overall impressions of the animals. The questionnaire was written in English and included 15 items describing behaviors representative for red deer with descriptions (Table 1). The raters judged the propensity of each individual to display each specific behavior on a 5-point scale, compiled as follows: 1- "Almost never", 2- "Very rarely", 3- "Occasionally", 4- "Quite a lot", 5- "Most of the time". The raters were instructed not to discuss their ratings with each other to avoid mutual

influence and interference. Every animal was rated by all three raters from December 2018 to January 2019.

2.3. Behavioral Observations

Observations were performed during three different situations: “normal” (i.e., no external stimuli), “feeding” (i.e., the animals compete for a limited amount of food), and “handling” (i.e., the animals undergo a situation of stress), between April and July 2018. During the “normal” and the “feeding” observations, the animals were observed in a group setting, whereas during the “handling” observations they were observed in an individual setting. All the observations were recorded on a voice recorder (model Olympus WS-811) and then transcribed using Microsoft Excel. Apart from the audio recordings, one session per week in “feeding” observations was also video-recorded (camera Garmin VIRB 360). These recordings were made available for the observers as extra video material references to help reliably score the animals’ behavior. Questionnaire raters acted as observers during “normal”, “feeding” and “handling” situations, thus their overall impression of the deer was based on all three situations.

During the “normal” observations, the animals were free to roam through the paddocks without being intentionally enticed by external stimuli. The deer fed predominantly on the pasture or at the hay racks available in the paddocks, described in more detail above. The focal observations of the animals took place in the morning, between 9.00 and 11.00 a.m. and they were performed between two and five times per week, with an average of three times per week. Each focal observation, carried out via continuous focal recording (Martin and Bateson 2007), lasted for 15 minutes with a maximum of three focal animals per day and each animal was observed once per month.

During the “feeding” observations, the animals were provided with additional food (i.e., a mixture of soy, oats and barley). The food was always presented in eight piles, to let the competition escalate without causing unnecessary opportunities for exacerbation. The focal observations of the animals ranged between 30 and 45 minutes and were carried out via continuous focal recording (Martin and Bateson 2007). Moreover, to obtain the hierarchy of the

group, our most experienced rater also performed some group observations during feeding time (a standard procedure described in Esattore et al. 2020), recording all the interactions among all the deer, from the presentation of the food until its depletion. Due to the fast pace and the simultaneity of the interactions in this context, yet the clear connotation of the interactions, we decided to rely on our most experienced rater for the data collection. Every animal was recorded once a month.

Both "feeding" and "normal" observations focused on all social interactions between the focal animal and the rest of the herd (i.e., threats, agonistic encounters, socio-positive interactions, play, other; summarized in Table 2), however, for the purpose of constructing a hierarchy, we especially focused on the socio-negative interactions (i.e., any attack, threat or fight which caused an apparent displacement of the approached individual) during the feeding time. Moreover, each of the observers paid attention to the activity patterns of the focal animal together with the associations and feuds between the focal and other individuals. During both "normal" and "feeding" observations, any interference between the observers was avoided. They performed their observations from different locations within the paddock. Each observer had a randomly generated observation schedule in which the order of observations of the deer was pre-defined for each observer, ensuring that the observations of the same individual deer did not overlap between observers.

The "handling" observations took place once per month. During these periods, the individuals were weighed and checked for their general condition, the blood samples were collected and the antlers were measured, all while the deer were in a restraining apparatus. All the deer involved in the study had been regularly exposed and accustomed to this procedure. During "handling", one of the observers scored the behaviors presented in a pre-prepared table *ad hoc* (Table 3), to provide a general impression of the emerging inter-individual behavioral differences. The behaviors scored were mutually exclusive and covered the five stages of the handling process (i.e., creation of a subgroup from the herd, isolation of the animal from the subgroup, weighing, handling in the restraining apparatus, release). We treated the behaviors as binary variables, scoring them as 0 (i.e., behavior not displayed during the handling) or 1 (i.e.,

behavior displayed during the handling), based on the observation of the deer's reaction to the handling.

2.4. Dominance Hierarchy

For the hierarchy construction, we calculated the Clutton-Brock Index (CBI) of dominance (Clutton-Brock et al. 1979) on the basis of the number of interactions won and lost by each of the individuals in "normal" and "feeding" situations, according to the formula $CBI=(B+\Sigma b+1)/(L+\Sigma l+1)$. Where, B represents the number of individuals that the focal male defeated in one or more interactions, Σb represents the total number of individuals (excluding the focal animal) that those represented in B defeated, L represents the number of individuals by which the male was defeated and Σl represents the total number of individuals (excluding the male) by which those represented in L were defeated.

2.5. Statistical Analyses

All statistical analyses were conducted with the R program for statistical computing, version 4.0.3 (R Core Team 2020). For initial statistical tests, we used original rating scores as given by our three observers and the CBI index of dominance, as calculated from the formula above. For personality assessment, we first ran an inter-rater reliability check for each variable (Table 4), using Fleiss' Kappa (package irr) (Gamer et al. 2012), which is suitable for ordinal categorical data (Seltmann et al. 2018). The Kappa values for each item can range from -1 (perfect disagreement) to +1 (perfect agreement). If the item's reliability showed statistical significance, the mean value among the three raters was used in subsequent analyses.

We created a correlation matrix to see if the data was well-correlated. To test for sampling adequacy, we ran the Kaiser-Meyer-Olkin test (KMO-test) and the Bartlett's Test of Sphericity [all functions from package psych (Revelle 2014)]. The analyses showed appropriate sampling adequacy (Kaiser-Meyer-Olkin measure; KMO=0.74; Bartlett's test of Sphericity, $p < 0.001$). We combined three approaches to assess the number of factors to retain in the factor solution

(Morton and Altschul 2019): i) eigenvalues > 1; ii) scree plot analysis and iii) Horn's Parallel Analysis with 10,000 iterations [package paran (Dinno 2012)]. We then ran a principal component analysis (PCA; package psych) with a Varimax rotation, to investigate how these items were associated with each other as components. We obtained the individual deer component scores from the PCA output (Figure 1). Due to our relatively small sample size, we repeated the analyses with two additional factor analyses. In particular, we further corroborated our results with Exploratory Factor Analysis (package psych; see Appendix, Table S1) and a Regularized Exploratory Factor Analysis (REFA) for small samples (Jung and Lee 2011) using the fungible package (Waller 2020) (see Appendix, Table S2).

Furthermore, we used Spearman's rank order correlations of the overall CBI index of each dear with the individual component scores of the obtained personality component (i.e., "Confidence/Aggressiveness", further explained in the Results). We then calculated the links between the CBI index of each individual and the mean scores across raters of the questionnaire items that we thought would be linked with the hierarchy (i.e., "confident", "aggressive" and "submissive") using the Spearman rank order correlations.

3. Results

3.1. Personality Assessment

We found that five out of fifteen items showed a high overall agreement of the trait ratings between raters, namely "active", "aggressive", "confident", "submissive" and "stubborn" (Table 3). The smallest value of Fleiss' Kappa was found in "playful" (Kappa = -0.128, $p = 0.345$), and the highest in "submissive" (Kappa = 0.432, $p < 0.001$). The repeatable items ranged from "confident" (Kappa = 0.284, $p < 0.01$) to "submissive" (Kappa = 0.432, $p < 0.001$). A scree plot test, with eigenvalues > 1, and a Horn's Parallel Analysis test with 10,000 iterations suggested 1 component (i.e., 1 factor) for the remaining five items. We entered these five items into further PCA analyses to investigate how they were associated with each other as components. The PCA-solution was Varimax rotated, and loadings > ±0.4 were considered salient. Most items had high communalities, apart from "active" (0.159), of which the low communality renders the item

unsuitable for contributing to PCA structure. PCA solution gave one principal component which explained 71.49 % of variance (Table 4). This component had high positive loadings of "aggressive" (0.888), "confident" (0.927) and "stubborn" (0.930), and high negative loadings of "submissive" (-0.950), thus, we labelled it as "Confidence/Aggressiveness". A separate EFA suggested the same personality model, which was further supported by REFA (see Table S1 and Table S2 in the Appendix, respectively, for more details).

3.2. Hierarchy Construction and Links between Personality and Dominance Hierarchy

We recorded a total of 534 inter-individual agonistic interactions (mean ± SD: 48.55 ± 24.41). The results of the CBI are shown in Table 5. The values ranged from 0.588 (i.e., an animal that was rarely involved in agonistic interactions and, when it was the case, lost them) to 4.5 (i.e., an animal which was rarely challenged, but was the winner of all the agonistic interactions even against other dominant individuals). Individual personality component scores were not correlated with the CBI score ($r_s = 0.45$, $p = 0.17$). The CBI score was, however, significantly linked to several adjective ratings that were connected with aggressiveness. Namely, we found a significant positive correlation between CBI and "confident" ($r_s = 0.66$, $p = 0.03$), and a significant negative correlation between CBI and "submissive" ($r_s = -0.68$, $p = 0.02$). The correlation between CBI and "aggressive" did not reach statistical significance ($r_s = 0.56$, $p = 0.14$).

4. Discussion

In this study we explored personality and its links to dominance hierarchy scores in captive adult male red deer. In particular, we created a novel personality questionnaire by consulting several previous questionnaires on Cervids and other mammal species, paying attention to, and creating, new items relevant for this species' behavioral repertoire, e.g., "Socially Anxious". Using a combination of both "bottom-up" and "top-down" approaches, we carefully selected 15 items. We found that only five of these 15 items showed an acceptable level of agreement between the raters, which overall corresponds to findings of behavioral consistency in other studies (Seltmann et al. 2018).

However, the observed between-rater agreement was much lower than in some other studies (e.g., Lloyd et al. 2007; Bergvall et al. 2011; Seltmann et al. 2018), which was an unexpected result. Given that descriptions of the items were kept simple and all three raters had several months of observational experience with all focal deer, such an exposure time should have been enough to reliably rate deer behavior. One explanation for the low agreement could be our relatively small sample size; with the possibility to rate more individuals it might have been possible to more reliably capture the variation in deer behavior (Sim and Wright 2005). Another explanation might be the difference in experience between the raters (Munch et al. 2019). Agreement has been demonstrably higher in behavioral ratings among novice raters when compared to expert raters (Munch et al. 2019). Even though two raters were acquainted and collected observational data for several months, the third rater still had more experience with the focal individuals. However, when re-analyzing our data and excluding the more experienced rater, Kappa values did not improve overall (see Appendix, Table S3), indicating an unlikely explanation for our findings. Perhaps the descriptions of these items did not adequately reflect the actual behavioral repertoire of the deer and should be revised and improved in the future (Koski 2011). The items with high agreement were related to general movement and antagonistic interactions that are usually easy to identify by observers (e.g., Meagher 2009). Nevertheless, four of the five items that showed acceptable agreement loaded on a single component, labelled "Confidence/Aggressiveness". This component contained items that were of antagonistic nature (positive loadings of "aggressive", "confident" and "stubborn" and negative loadings of "submissive"). Deer scoring high on "Confidence/Aggressiveness" have "*caused harm to other deer and humans, made quick decisions and often initiated interactions and displaced other deer*". Further, they "*did not readily give in or gave up on certain activities and did not turn away in interactions*". It is, however, safe to assume that the component describing variation in antagonistic items in red deer personality does not comprise their full behavioral variation, because we did not include items related to foraging or mate choice.

In general, individuality is a strong predictor of activity patterns in deer (Stache et al. 2013), their differences in neophobia (Monestier et al. 2017) and motivation to engage in fighting (Jennings, Hayden, and Gammell 2013). Moreover, individuality has ecological and evolutionary

consequences, since it has been linked to diverse life-history traits in wild roe deer (Debeffe et al. 2014; Monestier et al. 2015; Bonnot et al. 2020). The component "Confidence/Aggressiveness" found in red deer was similar to "Dominance" in fallow deer, where the items "aggressive" and "submissive" loaded highly on this component (Bergvall et al. 2011). The studies on other ungulate species found similar personality components that describe antagonistic or dominance-related behaviors, perhaps because the social rank is linked to life-histories (Favre, Martin, and Festa-Bianchet 2008) and is an important determinant of reproductive success in deer (Clutton-Brock et al. 1979). In our study, we only investigated male individuals, which are known to invest significant energy in attainment of a high rank. Aggressive and confident behavior might help male red deer to attain and keep high ranks, which in turn helps them gain access to resources and mates (Appleby 1980). It would be interesting to also assess female red deer to investigate the presence of a "Confidence/Aggressiveness", or perhaps a related "Dominance" personality component (i.e., as found in Bergvall et al. 2011).

The dominance hierarchy of our animals was assessed via repeated measures of focal behavior (Briffa, Sneddon, and Wilson 2015) and was roughly constant for the whole season. This usually happens among animals that know each other (Bartoš 1982) and where social dynamics do not suffer from unexpected events (e.g., a dominant deer suffers severe injuries or arrival of an unknown animal) (Clutton-Brock et al. 1979). Even though some animals were consistently more dominant than other animals, the hierarchy of our bachelor group was not linear, which is rare in this species (Appleby 1983; Bartoš and Bubenik 2011; but see Clutton-Brock, Clutton-Brock Guinness, and Albon 1982; Lincoln 1972; and Mitchell 1977 for linear hierarchies). Interestingly, not all dominant individuals perceived agonistic interactions in the same way (Esattore et al. 2020), and these inter-individual differences in interaction-proneness might be related to personality.

It has been suggested that if stable dominance hierarchies are an important part of the social structure of a species, behavioral expressions might be limited depending on the rank in the hierarchy (Verbeek et al. 1999; Creel et al. 1992). When an individual's position in the dominance hierarchies or status in the social group changes, we could expect that, the amount of their personality traits change as well (e.g., Rudin, Tomkins, and Simmons 2016; Dingemanse and de

Goede 2004; Šlipogor et al. 2021). Dominance hierarchies are often defined and maintained by agonistic interactions within the group. There are several factors influencing the motivation of an animal to begin or simply be involved in an agonistic encounter, including its self-perceived current quality, the value of the individuals in its surroundings and a winner/loser effect resulting from previous fights (Dingemanse and de Goede 2004; Jennings, Hayden, and Gammell 2013). Moreover, the individuals of a group can, to some extent, adapt their behavior to appropriately respond to the changing environmental stimuli (Coppens, de Boer, and Koolhaas 2010; Komers 1997) [e.g., social instability in an experimentally-induced new social environment (Esattore et al. 2020)]. For example, individuals with a lower expression of a specific behavioral trait may need to adapt their behavior to different environmental conditions (see "Compensatory hypothesis" in Betini and Norris 2012), whereas individuals with higher levels of a certain behavioral feature may achieve a sufficiently high level of fitness without the need to adjust their behavioral response to different social contexts or environmental conditions. Despite the behavioral fluctuations, it is likely that the individual characteristics of higher or lower expression of a behavioral trait will not be completely lost and will, to some extent, be maintained notwithstanding the modifications of the social environment (Esattore et al. 2020).

We did not find an overall link between “Confidence/Aggressiveness” personality scores and deer dominance hierarchy. However, we found positive links between the rank of the individuals and the antagonistic item “confidence” that loaded highly in the factor solution, promoting a more interaction-prone behavior. Namely, the individuals of higher rank were also assessed by the raters as more confident. Conversely, we found a negative link between the rank of the animal and the trait “submissive”, suggesting that individuals that ranked higher in the bachelor group had lower ratings of submissiveness. Dominance status is sometimes associated with specific personality traits, even though the nature of this relationship appears to be complex (Rudin, Tomkins, and Simmons 2016; Drent, Oers, and Noordwijk 2003). For example, the personality component “Confidence” was positively correlated to the dominance rank in Hanuman langurs (Konečná et al. 2008) and the trait “Dominance” was positively linked to dominance strength in mountain gorillas (Eckardt et al. 2015), but the dominance rank was not explaining variation in personality traits of female bonobos (Seyfarth, Silk, and Cheney 2012).

Furthermore, although "Aggressiveness" in graylag geese (*Anser anser*) was positively related to dominance rank (Kralj-Fišer, Weiß, and Kotrschal 2010), dominance was not related to boldness, exploration or activity in barnacle geese (Kurvers et al. 2009). Generally, individuals whose traits could be ascribed as proactive (i.e., those that score highly on "Aggressive" or "Confident") are more likely to initiate and win a physical contest (Sih, Bell, and Johnson 2004; Garnham et al. 2019), as the initiative is often associated with a positive outcome of the aggression (Favati, Leimar, and Løvlie 2014). Thus, more confident individuals will probably take greater risks in fights and, conversely, less confident individuals will be less interaction-prone (Briffa, Sneddon, and Wilson 2015). If this risk-prone attitude is shown repeatedly and consistently, the animal will be the winner of most of the fights, resulting in the animal's overt dominance over others. However, these findings are rare and still inconclusive (e.g., Fox et al. 2009). The link between personality traits and contest behavior is not always consistent, but it is often context-dependent (Dingemanse and de Goede 2004; Briffa, Sneddon, and Wilson 2015); therefore, the incorporation of further physiological data in the study of personality and dominance may perhaps help to further understand its complex nature (Briffa, Sneddon, and Wilson 2015; Briefer, Oxley, and McElligott 2015; Finkemeier et al. 2019) .

Our finding that the position of a red deer in the dominance hierarchy was linked to the variation in two items related to antagonistic interactions ("confident" and "submissive") is interesting for several reasons. First, a correlation between questionnaire items and scores from an index estimated by behavioral observations gives confidence that personality assessed via questionnaires does reflect real behavioral variation. Even though there is still some skepticism in the field about the use of trait ratings in animal personality research, a manifold of studies have shown a clear link between trait ratings and behavioral coding (Carter et al. 2012; Konečná et al. 2008; Weiss et al. 2011; Eckardt et al. 2015). Second, the personality items composing the personality trait "Confidence/Aggressiveness" seem to be linked to the dominance rank in male red deer in a similar manner to previous studies in deer and other species.

5. Conclusions

Although we attempted to carefully construct our personality questionnaire, the explanations of several items were possibly not clear enough to result in acceptable agreement between raters. Therefore, as a general note, more care should go into the construction of questionnaires for personality assessment. In addition, it might be advisable that raters have a high level of experience with the focal animals, more than the novice raters had in our study. Considering the found interrelationship between the long-term measures of personality items and dominance hierarchy in red deer, more data is needed to verify the findings of our study, in terms of the proximate mechanisms underlying variation in behavior and dominance hierarchies (e.g., stress: glucocorticoids; sex hormones: testosterone; autonomic nervous system: heart rate and heart rate variability).

Last, studies on different species either kept in zoos (Račevska and Hill 2017; Tetley and O'Hara 2012; Williams et al. 2019), or different facilities or farms (Forkman, Furuhaug, and Jensen 1995; Graunke et al. 2013; Veissier, Aubert, and Boissy 2012) have shown the importance of knowing the individual characteristics of the animals to implement the best strategy in guaranteeing their welfare (Robinson et al. 2017; Robinson et al. 2016; Freeman and Gosling 2010). As personality has not been largely considered in welfare management decisions, studies like this one could represent an important step forward in the development of this field.

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Table 1: Questionnaire items with their descriptions, together with Fleiss' Kappa and p-values across three raters.

Item	Description	Fleiss' Kappa	p-value
Active	The deer moves around a lot, often at a fast pace, spends little time being still	0.359	<0.001
(Socially) Anxious	The deer seems to be restless about everything and does not trust other individuals easily. It carefully controls the social surroundings	-0.075	0.455
Aggressive	The deer causes harm or potential harm to other individuals, both deer and human	0.301	<0.001
Bullying	A (larger) deer overreacts towards another animal of unbalanced size initiating a confrontational behavior without a specific reason	0.170	0.161
Calm	The deer does not get easily excited and reacts to change in a relaxed, unhurried way	-0.046	0.63
Confident	The deer behaves in an assured manner. It makes quick decisions and does not hesitate. It initiates the interactions and displaces other deer	0.284	<0.01
Excitable	The deer over reacts to any change, easily excited from outside disturbances and is not calming down easily	-0.0839	0.388
Friendly	The deer is not overly hostile towards others and initiates close contact to others within their group (scratching, rubbing , etc.) or lies/stands close to others (<2m) whilst resting.	-0.0806	0.416
Inquisitive	The deer readily explores new situations, objects, animals or people and tries to learn new things.	-0.0687	0.521
Opportunistic	The deer seizes a chance as soon as it arises.	0.00121	0.99
Playful	The deer initiates play and joins in when play is solicited.	-0.128	0.345
Slow/Non active	The deer moves and rests in a relaxed manner, moves slowly and deliberately, not easily hurried.	0.134	0.146

Solitary	The deer prefers to spend time alone and does not seek out contact with other deer.	0.063	0.514
Submissive	The deer gives in readily to others of a similar size and acts as though lower in rank to other deer; e.g., they will retreat or turn away in interactions.	0.432	<0.001
Stubborn	The deer does not give up easily on some activity	0.369	<0.001

Table 2: Categories, behaviors and their descriptions, scored during "feeding" and "normal" observations (based on Bartoš 1982; Clutton-Brock et al. 1982).

Category	Behavior	Description
Contact agonistic encounters	Chase	a subject runs after another
	Kick	a subject performs an attack using at least one of the legs
	Flail	two subjects standing on the back legs and kicking each other with the front
	Nibbling	a subject is browsing the other subject's fur, causes displacement
	Pushing	the subject pushes the other with the muzzle and pushes, causing displacement
	Biting	a subject bites another subject
Non-contact agonistic encounters	Head raise	a subject threatens the other raising the head towards the back
	Tongue out	a subject approaches the other while pulling out the tongue / grinding the teeth
	Ears back	a subject threatens the other moving the ears backward
	Imposition	a subject dominates the other putting the head over its back (T position)
	Direct look	a subject threatens the other moving the head toward the other and causing a displacement
	Standing threat	a subject stands on the back legs to threaten the other, without any attempt to kick
	Lips squishing	a subject squishes its lips
	Displacement	when the approach of a subject displaces the other without any specific threat or attack
Socio-positive interactions	Grooming	as "nibbling", without displacement
	Rubbing/Touching	the subject scratches its head over the other or touches it with the muzzle. No displacement
	Licking	Long-lasting licking of the other's fur. Similar to grooming, no displacement

Play	Playing	two subjects chase each other with no offensive purpose
Other	Mounting	a subjectmounts another subject (needs to be neither aggressive nor sexual)
	Avoidance	a subject avoids to get close to the other without engaging any kind of interaction

Table 3: The five stages of the handling process and behaviors scored during the process. Behaviors scored were mutually exclusive.

Handling process stages	Behavior
Pre-division	Leads the group when chased
	Stays behind when chased
	Turns back to the operators
	Stops when chased
	Chases the operators
Division	Attacks operator
	Threatens
	Turns when separate
	Hides/Lays down
	Goes spontaneously to the crush
	Avoids the operator
	Pushes/Attacks back the door
Weighing	Turns while on the loader
	Stays while on the loader
	Is afraid of entering
	Is not afraid of entering
Restraining apparatus	Vocalizes
	Stays in the crush
	Moves in the crush
	Moves when touched
	Stays when touched
	Pre-orbital opened
Release	Walks away
	Runs away
	Stops for a while

Table 4: Mean adjective loadings in a Principal Component Analysis solution. Varimax rotation with a Kaiser normalization. Communalities (H2) indicate each variable's proportion of variance explained by the components.

Item	Confidence/Aggressiveness	H2
Active	0.4	0.16
Aggressive	**0.89**	0.79
Confident	**0.93**	0.86
Submissive	**-0.95**	0.90
Stubborn	**0.93**	0.86

Figure 1: The individual component scores from the principal component “Confidence / Aggressiveness” for each deer.

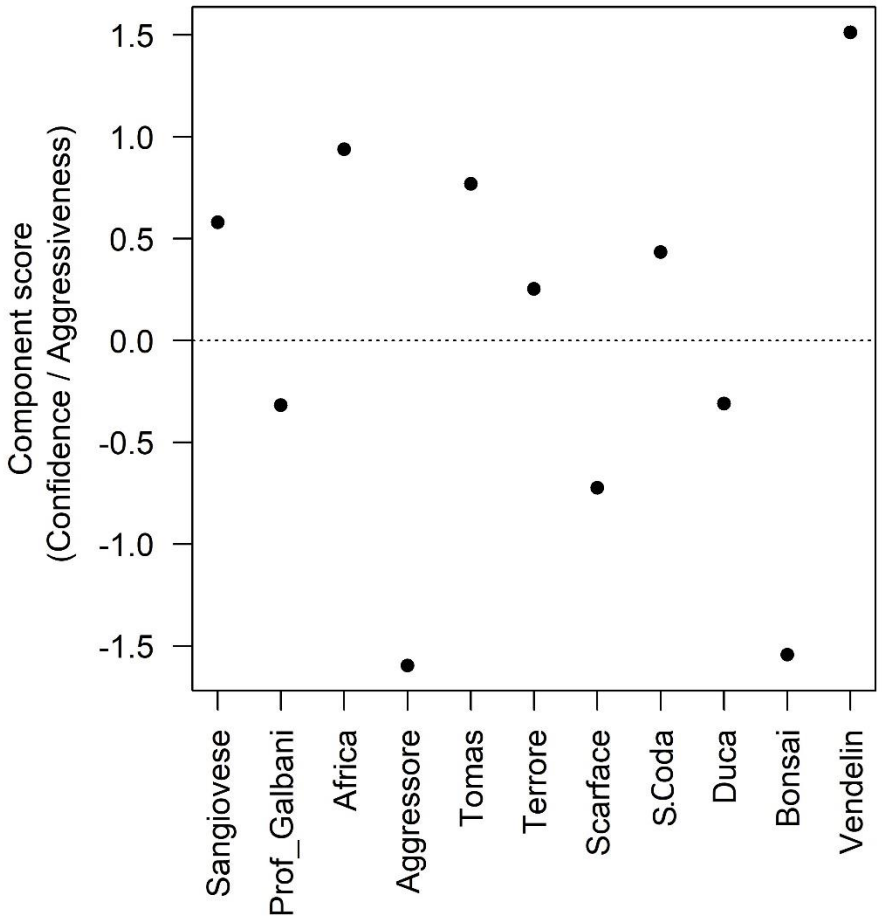

Table 5: Individuals of the group and their CBI index.

Deer	CBI
Vendelin	4.5
Bonsai	1.648
Scarface	1.446
Terrore	0.967
Duca	0.903
Africa	0.866
S.Coda	0.818
Tomas	0.736
Professor Galbani	0.723
Aggressore	0.698
Sangiovese	0.588

Appendix

Table S1: Standardized loadings from Exploratory (principal axis) Factor Analysis (EFA). Active does not load saliently (> ± 0.4) on the one factor. Other items load saliently on the factor, suggesting a similar structure as PCA. Model fit indices suggest very good fit of the 1-factor model to our data (RMSR = 0.04, RMSEA = 0). Communalities (H2) indicate each variable's proportion of variance explained by the factors.

Item	Factor 1	H2
Active	0.31	0.094
Aggressive	**0.84**	0.704
Confident	**0.91**	0.834
Submissive	**-0.96**	0.916
Stubborn	**0.91**	0.827

Table S2. Standardized loadings from Regularized Exploratory (regularized least squares) Factor Analysis (REFA). Active does not load saliently (> ± 0.4) on the one factor. Other items load saliently on the factor, suggesting a similar structure as PCA and EFA. Communalities (H2) indicate each variable's proportion of variance explained by the factors.

Item	Factor 1	H2
Active	0.31	0.09
Aggressive	**0.84**	0.70
Confident	**0.92**	0.84
Submissive	**-0.95**	0.91
Stubborn	**0.91**	0.82

Table S3: Fleiss' Kappa values for inter-rater consistency (only novice raters)

Item	Explanation	Fleiss' Kappa	p-value
Active	The deer moves around a lot, often at a fast pace, spends little time being still	0.610	< 0.01
(Socially) Anxious	The deer seems to be restless about everything and does not trust other individuals easily. It carefully controls the social surroundings	0.044	0.825
Aggressive	The deer causes harm or potential harm to other individuals, both deer and human	0.283	0.077
Bullying	A (larger) deer overreacts towards another animal of unbalanced size initiating a confrontational behavior without a specific reason	0.410	0.065
Calm	The deer doesn't get easily excited and reacts to change in a relaxed, unhurried way	-0.287	0.127
Confident	The deer behaves in an assured manner. It makes quick decisions and does not hesitate. It initiates the interactions and displaces other deer	0.064	0.684
Excitable	The deer over reacts to any change, easily excited from outside disturbances and is not calming down easily	0.200	0.288
Friendly	The deer is not overly hostile towards others and initiates close contact to others within their group (scratching, rubbing , etc.) or lies/stands close to others (<2m) whilst resting.	-0.172	0.332
Inquisitive	The deer readily explores new situations, objects, animals or people and tries to learn new things.	0.019	0.922
Opportunistic	The deer seizes a chance as soon as it arises.	-0.082	0.624
Playful	The deer initiates play and joins in when play is solicited.	-0.065	0.789
Slow/Non active	The deer moves and rests in a relaxed manner, moves slowly and deliberately, not easily hurried.	0.150	0.366
Solitary	The deer prefers to spend time alone and does not seek out contact with other deer.	0.078	0.684
Submissive	The deer gives in readily to others of a similar size and acts as though lower in rank to other deer; e.g., they will retreat or turn away in interactions.	0.511	< 0.01

Stubborn	The deer does not give up easily on some activity	0.364	0.051