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ORIGINAL ARTICLE

Biochemical responses to *Plasmodium* spp. infection in geese: alterations in acute phase reactants, redox balance, and serum proteins

Derya Kocamaz[1] · Oguz Merhan[2] · Gencay Taskin Tasci[3] · Kadir Bozukluhan[4]

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Abstract

Goose farming is gaining importance due to the economic value of meat and by-products; however, despite frequent reports of *Plasmodium* spp. infections in waterfowls, data on systemic biochemical responses in domestic geese remain limited. This study investigated biochemical alterations associated with natural *Plasmodium* spp. infection in *Anser anser domesticus*, focusing on acute phase proteins (APPs), thiol–disulfide homeostasis (TDH), and serum protein profiles. Blood samples were collected from geese with *Plasmodium* infection defined by combined microscopic examination and PCR (n = 35) and from uninfected geese (n = 20) Serum levels of APPs [Serum amyloid A (SAA), haptoglobin (Hp), total sialic acid (TSA)], TDH parameters [Native thiol (NT), total thiol (TT), disulfide (DS)], and serum proteins (total protein, albumin, globulin) were analyzed. *Plasmodium*-infected geese showed significantly higher levels of APPs than uninfected geese, indicating a strong acute phase response. Meanwhile, thiol components (TT, NT, DS) were significantly lower in *Plasmodium*-infected geese, reflecting infection-associated oxidative stress. However, redox ratios remained stable, suggesting preserved redox balance through compensatory antioxidant mechanisms. No significant differences were observed in serum protein concentrations. Correlation analysis revealed that Hp positively correlated with DS and negatively with NT/TT%, highlighting an interaction between inflammation and oxidative imbalance. Principal component analysis (PCA) showed that multivariate differentiation between infected and uninfected geese was mainly associated with protein-related and thiol-based redox parameters. In conclusion, *Plasmodium* infection triggers a distinct inflammatory and oxidative response in domestic geese, without affecting total serum protein levels. The combined use of APPs and TDH markers provides a promising non-invasive approach for monitoring infection-related physiological responses in avian malaria, supporting their potential utility in veterinary practice.

Keywords *Anser anser domesticus* · Avian malaria · Acute phase proteins · Oxidative stress · Thiol–disulfide homeostasis

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✉ Derya Kocamaz
drykocamaz@gmail.com

[1] Department of Biology, Faculty of Science and Arts, Cukurova University, 01330 Adana, Türkiye

[2] Department of Biochemistry, Faculty of Veterinary Medicine, Kafkas University, 36100 Kars, Türkiye

[3] Department of Parasitology, Faculty of Veterinary Medicine, Kafkas University, 36100 Kars, Türkiye

[4] Department of Internal Medicine, Faculty of Veterinary Medicine, Kafkas University, 36100 Kars, Türkiye

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Zusammenfassung

Biochemische Reaktionen auf *Plasmodium* spp.-Infektion bei Gänsen: Veränderungen der Akut-Phasen-Proteine, des Redox-Status und der Serumproteine

Die Gänsehaltung gewinnt aufgrund des wirtschaftlichen Werts von Fleisch und Nebenprodukten zunehmend an Bedeutung; trotz häufiger Berichte über *Plasmodium* spp.-Infektionen bei Wasservögeln sind die Daten zu systemischen biochemischen Reaktionen bei Hausgänsen jedoch begrenzt. In dieser Studie wurden die biochemischen Veränderungen im Zusammenhang mit einer natürlichen *Plasmodium* spp.-Infektion bei *Anser anser domesticus* untersucht, wobei der Fokus auf den Akut-Phasen-Proteinen (APPs), der Thiol-Disulfid-Homöostase (TDH) und den Serumproteinprofilen lag. Blutproben wurden von mittels kombinierter mikroskopischer Untersuchung und PCR-Analyse diagnostizierten *Plasmodium*-infizierten Gänsen (n = 35) sowie von nicht infizierten Gänsen (n = 20) entnommen. Die Serumspiegel der APPs [Serum-Amyloid A (SAA), Haptoglobin (Hp), Gesamtsialinsäure (TSA)], die Parameter der TDH [natives Thiol (NT), Gesamtthiol (TT), Disulfid (DS)] sowie die Serumproteine (Gesamtprotein, Albumin, Globulin) wurden analysiert. *Plasmodium*-infizierte Gänse wiesen signifikant höhere APPs-Spiegel auf als nicht infizierte Gänse, was auf eine ausgeprägte Akut-Phasen-Reaktion hinweist. Unterdessen waren die Thiol-Komponenten (TT, NT, DS) bei *Plasmodium*-infizierten Gänsen signifikant erniedrigt, was auf infektionsassoziierten oxidativen Stress hindeutet. Die Redox-Verhältnisse blieben jedoch stabil, was auf ein durch kompensatorische antioxidative Mechanismen aufrechterhaltenes Redox-Gleichgewicht hindeutet. Für die Serumproteinkonzentrationen wurden keine signifikanten Unterschiede festgestellt. Die Korrelationsanalyse ergab, dass Hp positiv mit DS und negativ mit NT/TT% korrelierte, was eine Wechselwirkung zwischen inflammatorischen Prozessen und oxidativem Ungleichgewicht nahelegt. Die Hauptkomponentenanalyse (PCA) zeigte, dass die multivariate Differenzierung zwischen infizierten und nicht infizierten Gänsen hauptsächlich mit proteinbezogenen und thiolbasierten Redoxparametern assoziiert war. Zusammenfassend zeigt diese Studie, dass eine *Plasmodium*-Infektion bei Hausgänsen eine ausgeprägte entzündliche und oxidative Reaktion auslöst, ohne dabei die Gesamtserumproteinkonzentrationen zu beeinflussen. Der kombinierte Einsatz von APPs- und TDH-Markern könnte einen vielversprechenden, nicht-invasiven Ansatz zur Überwachung infektionsbedingter physiologischer Reaktionen bei aviärer Malaria darstellen und damit eine ergänzende diagnostische Bedeutung in der Veterinärmedizin besitzen.

Introduction

Goose farming represents a growing segment of sustainable livestock production, particularly in developing countries. Although geese are among the earliest domesticated poultry species, they have not reached the commercial scale observed in chickens or ducks. Nevertheless, their remarkable adaptability to a wide range of climatic conditions supports their importance in selected regions of Asia and Europe (Buckland and Guy 2002). According to FAO data from 2022, goose farming is practiced in 40 countries, with an estimated global population of approximately 366 million birds. China dominates the global population, accounting for 87% of the total, followed by Mozambique (4.2%) and Myanmar (1.3%) (FAOSTAT 2022). Türkiye ranks eighth worldwide with 1.39 million geese, accounting for 0.38% of the global population, with the majority concentrated in the provinces of Kars (38%), Ardahan (9.5%), and Muş (4.3%) (TURKSTAT 2023).

Beyond their role in meat production, geese are economically valuable for foie gras, feathers, and fat. Goose feathers may reach market prices of 100–130 USD/kg, while goose fat is sold at higher prices than butter in certain European markets (FAOSTAT 2022; Karadag 2025). Considering the increasing global demand for high-quality animal protein, particularly in aging populations, goose meat has emerged as a nutritionally dense alternative (Wickramasinghe et al. 2020; Gurer 2021; Ambikapathi et al. 2022; Ederer et al. 2023). Moreover, geese show relatively high resistance to many common avian diseases, supporting their characterization as a low-risk and sustainable production model (Dumlu 2024). However, production systems that overlap with natural wetlands and migratory flyways place domestic geese in close proximity to wild waterbirds, making them a potentially informative model for understanding infection dynamics shared between wild and managed avian populations (García-Longoria et al. 2016).

Türkiye is located at the intersection of multiple climatic zones and phytogeographical regions, occupying a strategic position along major Afro–Eurasian migratory bird flyways (Ozkoc 2022). Consequently, the country hosts exceptionally high avifaunal diversity and is regarded as a pivotal region for pathogen circulation and transmission between migratory and resident birds (Ozkoc 2020). In eastern Türkiye, the province of Kars is characterized by diverse habitats ranging from high-altitude steppes and wetlands to lakes and river systems, supporting both wild waterbirds and extensive domestic goose farming. Notably, Kars functions as a critical ecological corridor encompassing internationally significant wetlands such as Lake Kuyucuk—a Ramsar Wetland of International Importance—and the Aras River Basin. A field survey conducted by Ozkoc (2020) recorded

193 bird species belonging to 51 families and 18 orders in Kars Province over a 50-day observation period, with Passeriformes, Charadriiformes, Accipitriformes, Anseriformes, and Pelecaniformes representing the most species-rich groups. The presence of large numbers of migratory birds during seasonal movements facilitates pathogen exchange between wild and domestic avian populations in this region (Ciloglu et al. 2020).

Haemosporidian parasites, including the genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*, represent some of the most widespread parasitic infections in wild bird populations (Tamayo-Quintero et al. 2023). Among these, *Plasmodium* spp., which are transmitted exclusively by mosquitoes (particularly *Culex* spp.), are the recognized causative agents of avian malaria worldwide (Santiago-Alarcon et al. 2012). Other haemosporidian genera are transmitted by different dipteran vectors, such as biting midges, louse flies, and blackflies, and are associated with malaria-like syndromes rather than avian malaria in the strict sense (Martínez-de la Puente et al. 2018; Adler and McCreadie 2019). Migratory birds play a key role in the long-distance dispersal of these parasites, facilitating their introduction into new geographical regions and host communities when suitable vector conditions are present (Perrin et al. 2025). Although active transmission is generally restricted to temperate and tropical zones, many haemosporidian lineages exhibit broad geographic distributions due to migratory host movements (Ciloglu et al. 2020).

Avian malaria is often asymptomatic in healthy birds; however, when parasites are introduced into naïve host populations or novel environments, significant pathogenic effects may occur, including population declines in endemic and endangered species (Atkinson et al. 2000). Although studies on the pathogenicity of *Plasmodium* infections in wild birds remain limited, experimental infections have demonstrated sudden mortality accompanied by pathological findings such as splenomegaly, hepatomegaly, and cardiomegaly (Ilgūnas et al. 2016). Furthermore, *Plasmodium*–infected wild birds have been shown to possess significantly shorter telomeres, a trait associated with reduced lifespan, highlighting the potential long-term fitness costs of infection (Asghar et al. 2015). These findings suggest that avian malaria may have consequences not only at the individual level but also for population dynamics and ecosystem stability. Increasing evidence also indicates that climate change and anthropogenic environmental pressures facilitate the spread of generalist pathogens such as *Plasmodium* spp. into new regions and host assemblages (Hernández-Ospina et al. 2024; Kim et al. 2025).

The Plasmodium parasite infects erythrocytes and various tissues, initiating with the injection of sporozoites and followed by merogony and gametogony (Atkinson and LaPointe 2009; Inci et al. 2012). Three infection stages have been described: the acute phase, during which hosts are initially infected; the chronic phase following survival of the acute stage (Ferrell et al. 2007); and the latent phase, characterized by a marked reduction or apparent clearance of parasites mediated by the host immune system (Valkiūnas et al. 2005). Parasite intensity typically peaks during the acute phase and is associated with reduced body mass, decreased hemoglobin levels, and impaired health condition (Alemneh et al. 2025). However, the impacts of haemosporidian infections are complex and may vary considerably among individuals and species depending on parasite lineage, environmental conditions, and host traits (Ferrell et al. 2007; Martinsen et al. 2008; Puente et al. 2010; Kim et al. 2025).

During the infection, the host's innate immune system is rapidly activated. In birds, as in mammals, this response involves the production of APPs such as SAA, Hp, and TSA (Nawaz et al. 2021; Janmohammadi et al. 2020). These proteins increase markedly during inflammation and serve as sensitive biomarkers of infection severity (Tetteh et al. 2021; Jamil et al. 2024). SAA functions as an apolipoprotein associated with high-density lipoproteins during inflammation and contributes to endotoxin detoxification, lymphocyte inhibition, and modulation of inflammatory cell trafficking (Urieli-Shoval et al. 2000). Hp, an α-globulin, binds free hemoglobin and limits oxidative damage resulting from hemolysis (Murata et al. 2004). TSA, which is frequently elevated during inflammatory conditions, is located at the terminal chains of glycoproteins and glycolipids and may serve as a complementary marker of the acute phase response due to its association with glycosylated APPs (Nazifi et al. 2011).

Alongside inflammation, oxidative stress represents a central feature of host–parasite interactions in avian malaria (Isaksson et al. 2013). Activated immune cells generate reactive oxygen species (ROS) that damage not only parasites but also host tissues (Erol et al. 2022). This process leads to disturbances in TDH, which is considered a sensitive and dynamic indicator of oxidative status. Thiol groups (–SH), when oxidized, form disulfide bonds, and the ratios among NT, TT, and DS, as well as DS/NT, DS/TT, and NT/TT ratios, are widely used to assess redox regulation (Erel and Neselioglu 2014). These parameters provide valuable insight into the oxidative environment induced by *Plasmodium* infection.

Moreover, infection-associated inflammation and oxidative imbalance also influence protein metabolism. Albumin, a major negative acute phase protein, typically decreases during inflammation, whereas globulins, including immunoglobulins and positive APPs, tend to increase (Cray et al. 2009; Sheinenzon et al. 2021). Alterations in serum total protein, albumin, globulin, and the albumin/globulin ratio can reflect nutritional status, hepatic function, and immune

activity (Washington and Van Hoosier 2012; Pekmezci and Cakir 2020).

Despite increasing interest in avian malaria, most biochemical studies have focused on passerines or poultry species such as chickens and ducks (Harr 2002; McDougald et al. 2020). In contrast, geese, which belong to waterfowl and occupy an important ecological interface between wild and domestic avian populations, remain underrepresented in studies examining systemic responses to *Plasmodium* spp. infection. Although several investigations have addressed morphological or molecular aspects of avian malaria, comprehensive biochemical profiling of inflammatory, oxidative, and metabolic alterations in geese is currently lacking (Wiersch et al. 2007; Valkiūnas and Iezhova 2018). To address this gap, we hypothesized that *Plasmodium* infection in geese is associated with coordinated alterations in APPs, TDH, and serum protein profiles, reflecting an integrated systemic inflammatory and oxidative stress response. To our knowledge, this study is the first to simultaneously evaluate APPs, oxidative stress indicators, and protein metabolism biomarkers in domestic geese (*Anser anser domesticus*) naturally infected with *Plasmodium* spp. By integrating SAA, Hp, TSA, NT, TT, DS, thiol–disulfide ratios, total protein, albumin, globulin, and the albumin/globulin ratio, this study provides a comprehensive biochemical overview of host–parasite interactions in naturally infected geese. The primary objective was to characterize the biochemical responses associated with *Plasmodium* infection in geese, with a particular focus on identifying potential diagnostic or prognostic biomarkers related to inflammation, oxidative stress, and protein metabolism. These findings may contribute to a deeper understanding of avian malaria pathophysiology and support future disease monitoring and health management strategies in waterfowl.

Materials and methods

Study area and sample collection

This study was conducted in Kars Province, Northeastern Türkiye (40°36′04.82″N, 43°05′50.83″E), a region characterized by the highest density of goose farming in the country. The area represents an important landscape featuring extensive domestic goose production and wetlands that support diverse wild waterbird populations. In November 2015, blood samples were collected from 400 domestic geese raised for commercial slaughter. According to regional husbandry practices, all sampled birds were approximately 180–200 days old and consisted exclusively of female individuals. All birds were clinically examined prior to sampling, and only individuals without visible signs of systemic disease were included in the study. Blood samples were obtained prior to slaughter from the *vena subcutanea ulnaris* into 10 mL anticoagulant-free tubes. For each individual, blood was divided into aliquots for serum separation, blood smear preparation, and molecular analyses. Samples were centrifuged at 3000 rpm for 15 min, and sera were aliquoted and stored at − 80 °C until biochemical analyses without repeated freeze–thaw cycles. All serum samples were stored under identical controlled conditions to preserve sample integrity.

Parasitological screening

Parasitological screening of the sampled geese was performed during the same sampling period as previously described by Tasci et al. (2018). Briefly, blood smears were examined microscopically for the presence of *Plasmodium* spp., and molecular screening for *Haemoproteus/Plasmodium* parasites was conducted using nested PCR targeting the mitochondrial cytochrome *b* (*cyt b*) gene. Detailed descriptions of smear preparation, PCR protocols, sequencing procedures, and parasite lineage identification are provided in Tasci et al. (2018) and are therefore not repeated here. Microscopic examination was performed using duplicate blood smears per individual and confirmed by repeated observations, identifying *Plasmodium* infection in 48 out of 400 geese. Molecular screening by nested PCR detected *Haemoproteus/Plasmodium* DNA in 145 samples. Sequencing of *mt-cyt b* fragments obtained from a representative subset of PCR-positive individuals revealed two *Plasmodium* lineages (KVPlm1–2), as previously reported (Tasci et al. 2018). All PCR analyses were conducted in triplicate for each sample to ensure amplification reliability. The present study uses these previously generated parasitological data solely to define infection status for subsequent biochemical analyses and does not include additional parasitological screening. Accordingly, the focus of the current work is on systemic biochemical responses associated with microscopically and PCR-confirmed *Plasmodium* infection, rather than on parasite detection, prevalence estimation, or lineage characterization.

Experimental groups

Infection status was strictly defined through the integration of microscopic and molecular diagnostic criteria. Individuals were categorized as infected only if *Plasmodium* was identified in Giemsa-stained blood smears and subsequently confirmed by PCR analysis. Accordingly, a subset of 35 geese meeting both criteria was assigned to the infected group. The uninfected group comprised 20 geese in which no detectable *Plasmodium* stages were observed in blood smears and which yielded negative results in all PCR screenings. This stringent classification approach was adopted to ensure

that the biochemical profiles specifically reflected systemic responses associated with microscopy- and PCR-confirmed *Plasmodium* infections. Furthermore, this dual-verification strategy was implemented to minimize the risk of misclassification arising from cross-reactivity with non-*Plasmodium* haemosporidian parasites.

Biochemical parameters and rationale

Although *Plasmodium* spp. infections in birds are primarily diagnosed using peripheral blood smears and molecular techniques, these approaches provide limited information regarding the host's systemic physiological response to infection. To evaluate infection-associated inflammatory and oxidative alterations, protein-based biochemical markers were selected based on their reliability and widespread use in domestic, wild and poultry avian species (O'Reilly and Eckersall 2014; Nazifi et al. 2011). Accordingly, APPs, including SAA and TSA, were selected to assess the systemic inflammatory response. In parallel, TDH parameters were employed as dynamic indicators of oxidative stress, given that protein thiol groups constitute a major component of plasma antioxidant defense and are highly sensitive to redox imbalance. Therefore, NT, TT, and DS levels, together with their derived ratios were analyzed to characterize redox dynamics associated with *Plasmodium* infection. Additionally, serum total protein, albumin, and globulin concentrations were measured to evaluate potential infection-related alterations in protein metabolism. Collectively, these biochemical markers provided an integrated assessment of inflammatory status, oxidative stress, and protein homeostasis in the study groups.

Acute phase proteins

SAA levels were determined using a solid-phase sandwich enzyme-linked immunosorbent assay (ELISA) according to the manufacturer's instructions (Phase™ Range SAA kit, Tridelta Development Ltd., Ireland). Microtiter wells were pre-coated with a monoclonal antibody specific for SAA. Serum samples and standards were added to the wells together with a horseradish peroxidase-conjugated anti-SAA monoclonal antibody, enabling simultaneous capture and labeling of SAA in a one-step procedure. Following incubation for 1 h at 37 °C and subsequent washing steps, 3,3′,5,5′-tetramethylbenzidine substrate solution was added and incubated for 15 min at room temperature. The reaction was terminated using a stop solution, and absorbance was measured at 450 nm using a microplate spectrophotometer (Epoch, BioTek Instruments, USA). TSA levels were quantified using a colorimetric spectrophotometric method based on the procedure described by Sydow (1985). Sialic acid residues bound to serum glycoproteins and glycolipids were liberated by acid hydrolysis with perchloric acid and reacted with Ehrlich's reagent to form a chromogenic complex. The absorbance was measured at 525 nm (Shimadzu UV-1700, Japan). TSA concentrations were calculated using a standard calibration curve generated from sialic acid standards (Millipore, USA).

Oxidative stress markers

TDH was evaluated as a redox-sensitive indicator of oxidative stress using commercial assay kits (Rel Assay Diagnostics, Türkiye), following the method described by Erel and Neselioglu (2014). Dynamic disulfide bonds present in serum samples were first reduced to free thiol groups using sodium borohydride, after which excess reducing agent was neutralized to prevent interference with subsequent reactions. Both newly reduced thiols and pre-existing native thiols were then reacted with 5,5′-dithiobis-(2-nitrobenzoic acid). This procedure enabled the determination of TT levels, while NT levels were measured directly without the reduction step. DS concentrations were calculated as half of the difference between TT and NT values. The following indices were subsequently calculated to evaluate redox balance: DS/NT, DS/TT, and NT/TT.

Serum protein profile

Serum total protein and albumin concentrations were measured using commercial colorimetric assay kits (Biolabo, France) on a microplate spectrophotometer (Epoch, BioTek Instruments, USA). Total protein levels were determined using the Biuret method, based on the reaction of peptide bonds with Cu^{2-} in an alkaline medium to form a violet-colored complex, with absorbance measured at 550 nm. Albumin concentrations were assessed using the bromocresol green dye-binding method at pH 4.2, with absorbance measured at 630 nm. Globulin concentrations were calculated by subtracting albumin values from total protein concentrations.

Statistical analysis

All biochemical assays were performed in triplicate, and the resulting mean values were used for statistical analyses. Data normality and homogeneity of variances were assessed using the Shapiro–Wilk and Levene's tests, respectively. For variables meeting normality assumptions, differences between *Plasmodium*-infected and uninfected geese were evaluated using the independent samples *t*-test. When data did not conform to normal distribution, the non-parametric Mann–Whitney *U* test was applied. Pearson correlation analysis was employed to examine relationships among biochemical parameters. In addition, PCA was conducted

to visualize multivariate patterns and to evaluate the relative contribution of individual variables to total variance. Principal component scores (PC1 and PC2) were subsequently compared between *Plasmodium*-infected and uninfected geese using independent samples *t*-tests to assess group differences along the major axes. Statistical significance was set at $p \leq 0.05$. Results are presented as mean ± standard deviation (SD). All analyses were performed using GraphPad Prism version 10 (GraphPad Software, USA).

Results

Acute phase proteins

APPs in *Plasmodium*-infected geese showed significantly higher values compared to uninfected geese. SAA concentrations were significantly higher in the *Plasmodium*-infected geese (2.89 ± 0.41 µg/mL) than in uninfected geese (2.22 ± 0.84 µg/mL; $t(53) = -3.69$, $p = 0.0005$, $d = 0.98$), indicating a large effect size. TSA values were also significantly higher in *Plasmodium*-infected geese (60.17 ± 10.14 mg/dL) compared with uninfected geese (52.43 ± 8.98 mg/dL; $t(53) = -2.91$, $p = 0.0056$, $d = 0.81$). Similarly, Hp levels were significantly higher in *Plasmodium*-infected geese (0.12 ± 0.03 g/L) than in uninfected geese. (0.09 ± 0.06 g/L; $t(53) = -2.32$, $p = 0.0283$, $d = 0.70$) (Fig. 1).

Oxidative stress markers

The analysis of thiol–disulfide balance revealed significant alterations between *Plasmodium*-infected and uninfected geese, indicating a systemic oxidative response associated with parasitic infection. TT levels were significantly lower in *Plasmodium*-infected geese (237.25 ± 34.63 µmol/L) than in uninfected geese (279.81 ± 42.48 µmol/L; $t = 3.80$, $p = 0.0006$, $d = -1.10$),

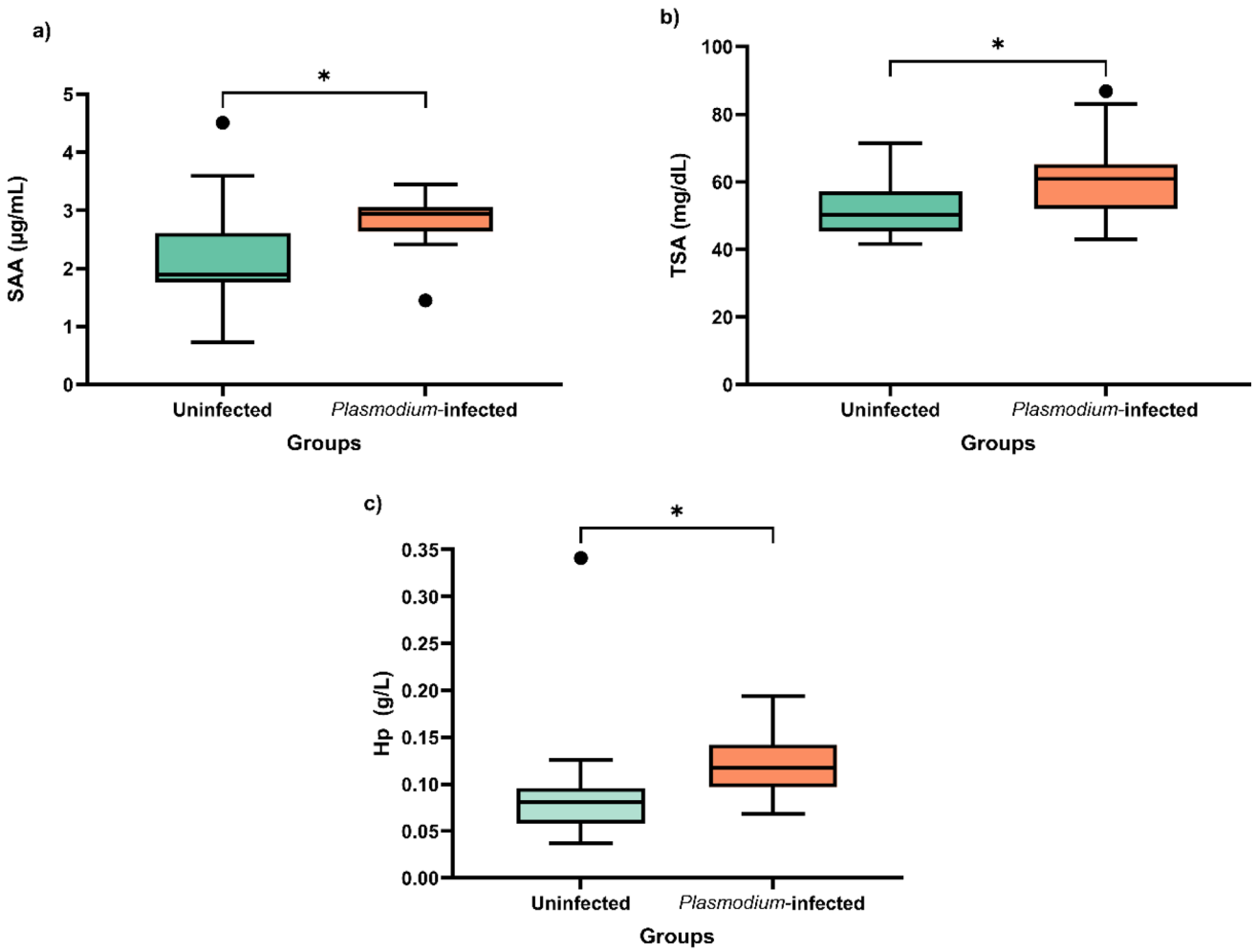


Fig. 1 Boxplots showing the levels of APPs in *Plasmodium*-infected and uninfected geese. **a** SAA (µg/mL), **b** TSA (mg/dL), **c** Hp (g/L). Statistically significant differences between groups are indicated by asterisks ($p \leq 0.05$)

reflecting a reduced thiol-based antioxidant capacity (Fig. 2). Similarly, NT levels were significantly lower in *Plasmodium*-infected geese (172.87 ± 33.37 µmol/L) compared to uninfected geese (198.70 ± 41.85 µmol/L; $t = 2.36$, $p = 0.0245$, $d = -0.68$). DS levels were also significantly lower in *Plasmodium*-infected geese (32.19 ± 13.44 µmol/L) than in uninfected geese (40.56 ± 12.80 µmol/L; $t = 2.28$, $p = 0.0280$, $d = -0.64$). In contrast, thiol/disulfide ratios did not differ significantly between groups: DS/NT% = 21.73 ± 9.48 in uninfected geese vs. 19.94 ± 10.57% in *Plasmodium*-infected geese ($t = 0.64$, $p = 0.5235$, $d = -0.18$), DS/TT% = 14.62 ± 4.24 in uninfected geese vs. 13.51 ± 5.16 in *Plasmodium*-infected geese ($t = 0.85$, $p = 0.3970$, $d = 0.23$), NT/TT% = 70.76 ± 8.49 in uninfected geese vs. 72.98 ± 10.32 in *Plasmodium*-infected geese ($t = -0.85$, $p = 0.3970$, $d = 0.23$).

Serum protein profile

There were no statistically significant differences in total protein, albumin, or globulin concentrations between *Plasmodium*-infected and uninfected geese. The albumin level in *Plasmodium*-infected geese was 1.88 ± 0.30 g/dL, compared to 1.92 ± 0.29 g/dL in uninfected geese ($t = 0.52$, $p = 0.6085$, $d = -0.13$). Similarly, globulin concentrations were comparable (2.83 ± 0.68 g/dL in *Plasmodium*-infected geese vs. 2.87 ± 0.30 g/dL in uninfected geese; $t = 0.25$, $p = 0.8061$, $d = -0.08$), as were total protein levels (4.71 ± 0.56 g/dL in *Plasmodium*-infected geese; 4.79 ± 0.30 g/dL in uninfected geese; $t = 0.65$, $p = 0.5180$, $d = -0.17$). The albumin to globulin ratio also remained unchanged between groups.

Correlation analysis

To explore the interrelationships among the measured biomarkers, Pearson correlation analysis was conducted and

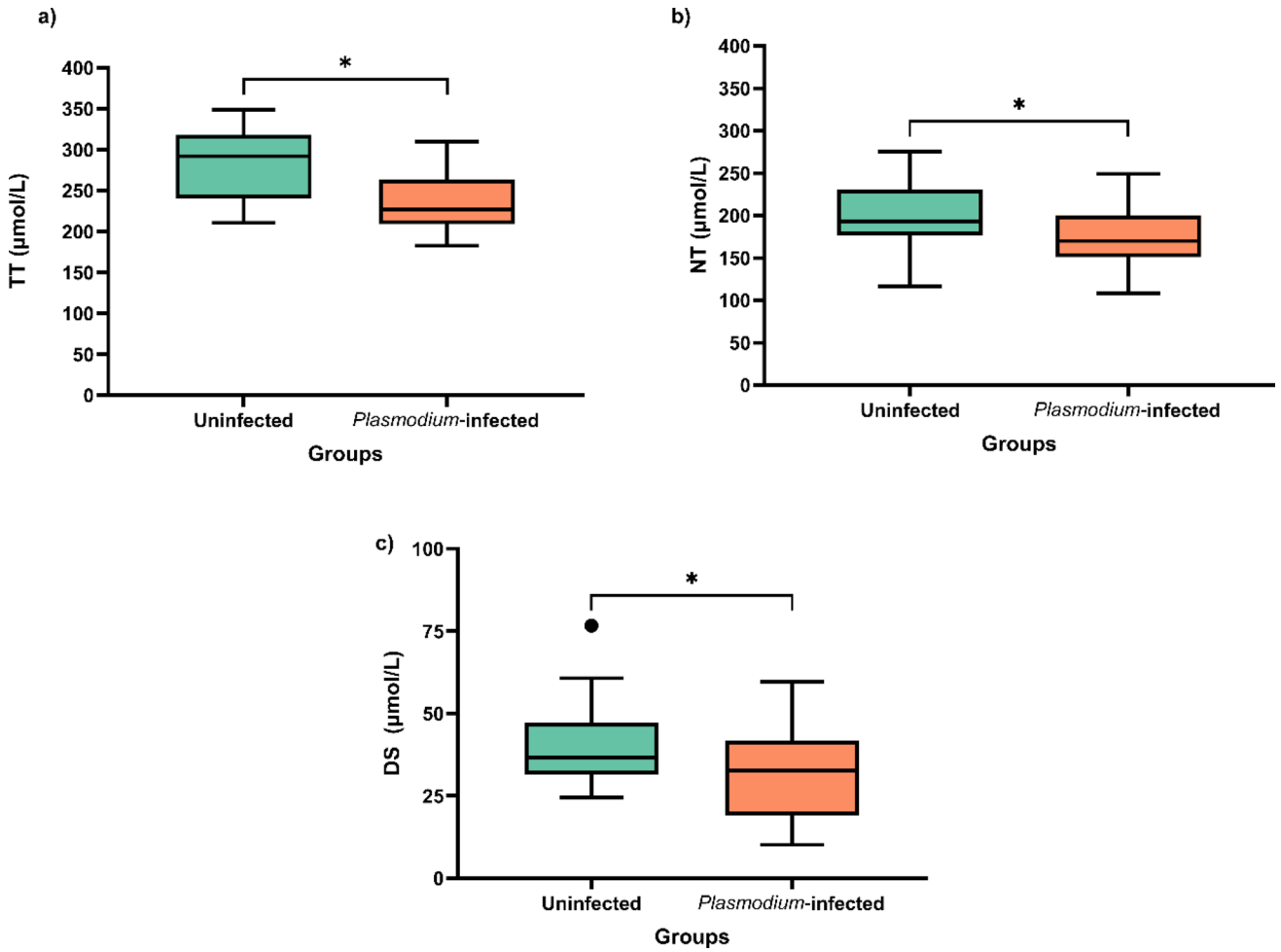


Fig. 2 Boxplots showing redox balance parameters in *Plasmodium*-infected and uninfected geese. **a** TT (µmol/L), **b** NT (µmol/L), **c** DS (µmol/L). Statistically significant differences between groups are indicated by asterisks ($p \leq 0.05$)

indicated in Fig. 3. Among APPs, Hp exhibited a significant positive correlation with DS (r = 0.393, $p = 0.019$), DS/NT% (r = 0.387, $p = 0.021$), and DS/TT% (r = 0.356, $p = 0.036$), while showing a negative correlation with NT/TT% (r = − 0.356, $p = 0.036$). These associations indicate a potential link between inflammation-induced Hp elevation and thiol-disulfide redox imbalance. In the TDH profile, TT was positively correlated with NT (r = 0.679, $p < 0.0001$) and DS (r = 0.449, $p \leq 0.0001$). NT was negatively correlated with DS (r = − 0.352, $p = 0.038$), DS/NT% (r = − 0.657, $p = 0.00001$), and DS/TT% (r = − 0.653, $p = 0.0005$), but positively associated with NT/TT% (r = 0.653, $p = 0.0001$). Additionally, DS showed strong positive correlations with DS/NT% (r = 0.904, $p = 0.0001$) and DS/TT% (r = 0.908, $p = 0.0001$), while being negatively correlated with NT/TT% (r = − 0.984, $p = 0.0001$). As expected, DS/NT% was positively correlated with DS/TT% (r = 0.904, $p = 0.0001$), and strongly negatively with NT/TT% (r = − 0.94, $p = 0.0001$). Moreover, DS/TT% showed a perfect inverse correlation with NT/TT% (r = − 1.000, $p \leq 0.00001$), confirming their reciprocal relationship. Regarding serum protein profile, a strong negative correlation was observed between albumin and globulin (r = − 0.584, $p = 0.0002$), whereas total protein was positively correlated with globulin (r = 0.902, $p = 0.0001$). These findings reflect the typical shift in serum protein fractions under inflammatory stress, where albumin levels decrease and globulin levels increase, thereby affecting overall protein balance. Notably, no statistically significant correlations were observed between the remaining APPs (SAA and TSA) and total serum proteins, nor among the TDH biomarkers.

Principal component analyses

PCA was performed to explore the multivariate relationships among APPs, TDH parameters, and serum proteins in *Plasmodium*-infected and uninfected geese. The first two principal components (PC1 and PC2) accounted for 36.2% and 19.7% of the total variance, respectively, collectively explaining 55.9% of the overall variability (Fig. 4). PC1 was primarily driven by derived thiol–disulfide indices, with strong positive loadings for DS/NT (%) and DS/TT (%) along with DS levels, while NT and the NT/TT (%) ratio exhibited negative loadings. Although a visual trend was observed along the PC1 axis in the biplot, statistical analysis of PC1 scores revealed no significant difference between *Plasmodium*-infected and uninfected geese ($t = 0.60$, $p = 0.548$, $d = 0.17$; Figure S1 in Supplement). In contrast, PC2 captured variation primarily associated with infection-related biochemical changes. TT, NT, DS, and albumin contributed to positive loadings on PC2, whereas total protein, globulin, TSA, Hp, and SAA showed strong negative contributions. Statistical comparison of PC2 scores demonstrated a highly significant difference between the study groups ($t = 4.35$, $p = 0.00006$, $d = 1.22$). These results indicate that infection-associated shifts in protein homeostasis, the acute-phase response, and redox-related parameters are primarily represented along this axis. Overall, while thiol–disulfide ratios contributed substantially to the total

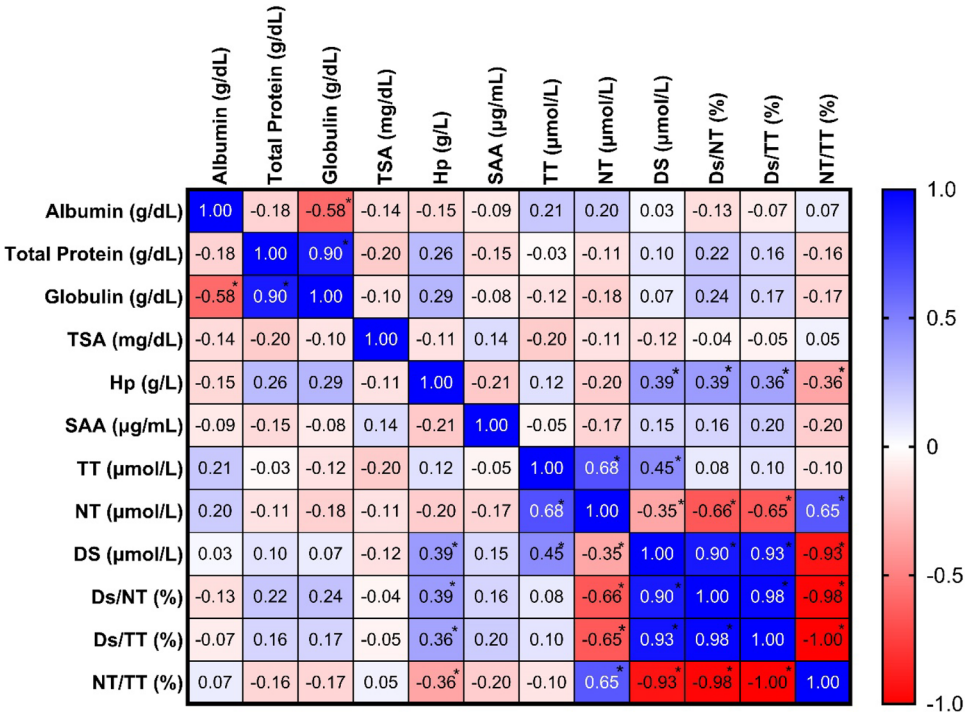


Fig. 3 Pearson correlation heatmap of APPs, TDH markers, and serum protein parameters in in *Plasmodium*-infected geese. Color intensity reflects the strength and direction of correlations (red = negative, blue = positive), and statistically significant correlations ($p \leq 0.05$) are marked with an asterisk (*) (color figure online)

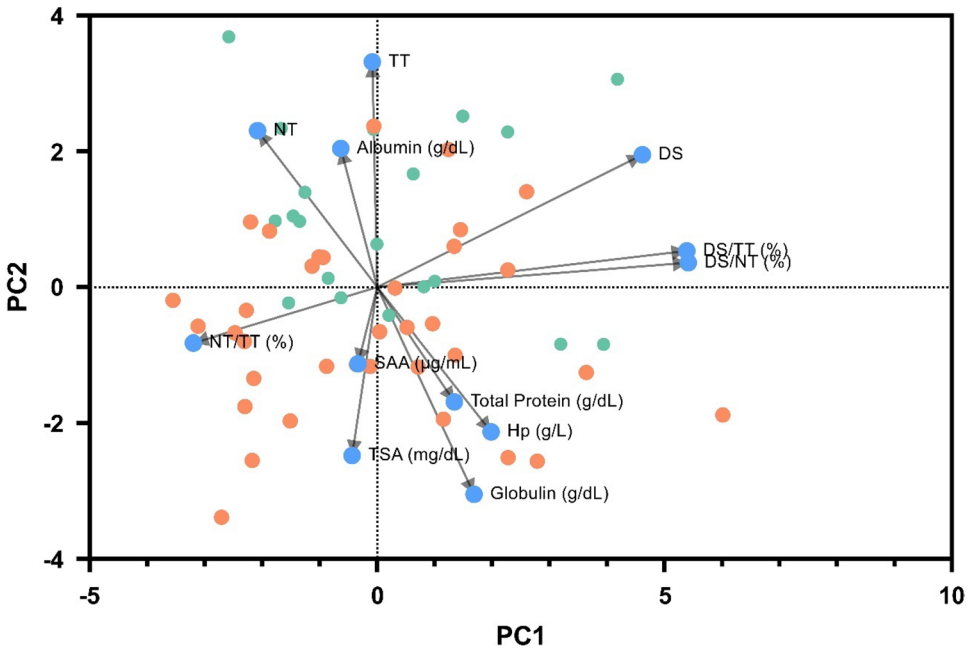


Fig. 4 PCA biplot of APPs, TDH parameters, and serum protein variables in *Plasmodium*-infected and uninfected geese. Individual samples are shown as points representing uninfected geese (green) and *Plasmodium*-infected geese (orange). Variable loadings are indicated by arrows (blue), illustrating the contribution and direction of each biochemical parameter along the first two principal components (PC1 and PC2) (color figure online)

variance (PC1), the statistically supported multivariate discrimination between *Plasmodium*-infected and uninfected geese was predominantly explained by PC2.

Discussion

In animals, systemic responses to infection are commonly characterized by activation of the acute phase response and redox imbalance, reflecting coordinated inflammatory and oxidative processes (Razavi et al. 2024).

In this study, *Plasmodium* infection in geese was associated with a distinct biochemical response profile involving activation of the acute phase response and alterations in thiol-based antioxidant capacity. The elevation of APPs (SAA, Hp and TSA) observed in infected geese is consistent with the activation of a systemic inflammatory response, whereas the concomitant reductions in thiol components (TT, NT and DS) support the presence of infection-associated oxidative stress at the cellular level (Merhan and Bozukluhan 2022). Notably, the lack of significant changes in thiol–disulfide ratios (DS/NT%, DS/TT%, NT/TT%) suggests that overall redox homeostasis is largely maintained, potentially reflecting compensatory activation of the host's antioxidant defense mechanisms rather than a complete disruption of redox balance (Delhaye et al. 2016). Similarly, the absence of significant alterations in albumin, globulin, and total protein levels suggests that *Plasmodium* infection did not result in a marked systemic alteration of protein metabolism, or that any potential effects were effectively buffered through regulatory mechanisms. Taken together, these findings indicate that *Plasmodium* spp. infection in geese is primarily associated with inflammatory and oxidative pathways, while physiological systems such as protein synthesis and metabolic regulation, which may be affected at later stages, appear to remain stable under the conditions examined. The observed biochemical profile in this study, characterized by increased acute phase proteins and altered thiol-based antioxidant defenses, is consistent with patterns previously reported in infected birds (Jiménez-Peñuela et al. 2023; Cellier-Holzem et al. 2010). Therefore, this response profile may be compatible with a subclinical stage of infection; however, this interpretation should be approached with caution in the absence of direct information on infection timing.

Acute phase proteins (APPs) are widely used biomarkers of inflammation in veterinary medicine and are routinely applied as diagnostic and prognostic indicators (Schrödl et al. 2016). Changes in circulating APP concentrations reflect systemic inflammatory activation and contribute to the assessment of infection-associated immune responses (Bozukluhan and Merhan 2023). Among positive APPs, SAA and Hp are known to exhibit pronounced increases during infectious processes. In avian species, elevated SAA concentrations have been consistently reported in association with acute inflammatory stimuli across different host species and pathogen types (Cray et al. 2009; Merhan and Bozukluhan 2022). Notably, increased serum SAA levels have also been documented in geese during experimentally induced acute phase responses, supporting the relevance of this marker in Anseriformes (Kovács et al. 2007), as well as in poultry species exposed to bacterial, viral, or sterile inflammatory challenges (Chamanza et al. 1999; Nazifi et al. 2011; Kromann et al. 2023).

Sialic acids are terminal components of glycan chains on glycoproteins and glycolipids and constitute physiological components of animal serum (Schauer 1985; Corfield and Schauer 1982). Circulating sialic acid concentrations have been reported to vary under conditions such as inflammation, infection, and tissue damage (Ekin et al. 2003; Makimura and Usui 1990). Although the underlying mechanisms are not fully elucidated, increased serum sialic acid levels are suggested to reflect the glycosylated structure of certain acute phase proteins, particularly α1-acid glycoprotein, released from the liver in response to inflammatory stimuli (Crook 1993). In addition to their role as inflammatory indicators, sialic acids may also function as receptors during pathogen attachment to host cells, and avian *Plasmodium* species have been suggested to interact with sialylated host structures during infection (Martin et al. 2005; Jankowski et al. 2019). Consistent with previous animal studies, in the present study, *Plasmodium*-infected geese exhibited significantly higher SAA, TSA, and Hp levels compared with uninfected geese (Seifi et al. 2014; O'Reilly et al. 2018; Messina et al. 2022). These findings indicate that the host organism mounted a robust acute phase response against *Plasmodium* infection, and that this response became detectable at the systemic level through sialylated glycoproteins. The observed increase in TSA is therefore likely related to the abundance of sialylated acute phase glycoproteins, reflecting inflammatory activity rather than serving as a direct measure of parasite invasion. Previous studies reporting interactions between *Plasmodium* and erythrocytic sialic acid structures further support the relevance of sialic acids in host–parasite interactions and host defense processes, although such associations should be interpreted cautiously in the absence of temporal or mechanistic data (Kumar and Rizvi 2013; Jankowski et al. 2019).

Oxidative stress plays an important role in the pathophysiology of infectious diseases as a result of disruption in the balance between infectious agents and host antioxidant defense systems, and its involvement in malaria infections is well documented (Percário et al. 2012). In *Plasmodium* infections, potential sources of oxidative burden include reactive oxygen species generation associated with intracytic hemolysis and immune cell activation (Plewes et al. 2014; Aqeel et al. 2021). Among the biomarkers used to evaluate oxidative stress, TDH has gained increasing attention as a dynamic indicator of redox status (Merhan and Bozukluhan 2022). Protein thiol groups constitute major antioxidant components of plasma, and alterations in thiol–disulfide balance have been reported in various pathological conditions characterized by oxidative or inflammatory stress (Bozukluhan and Merhan 2023; Georgescu et al. 2022). TDH reflects the reversible oxidation of native thiols to disulfides and provides insight into cellular redox regulation (Erel and Erdogan 2020; Jiang et al. 2021). The main parameters used to assess TDH include NT, TT, and DS, and changes in these parameters have been described in a range of infectious and inflammatory conditions in veterinary medicine (Surai et al. 2021; Balik et al. 2023). Disruptions in TDH have also been reported in avian infectious diseases, including viral infections in poultry, where oxidative stress-related alterations accompany infection. Reduced antioxidant enzyme activities have been observed in Marek's disease virus–infected chickens (Rajiv Kishore et al. 2017), and infectious bursal disease virus infection has been associated with increased intracellular reactive oxygen species production, decreased glutathione levels, and enhanced lipid peroxidation (Rehman et al. 2018). In the present study, TT, NT, and DS concentrations were significantly lower in *Plasmodium*-infected geese compared with uninfected geese. In contrast, thiol/disulfide ratios (DS/NT, DS/TT, NT/TT) did not differ significantly between groups. These findings suggest that although the infection induces a substantial oxidative burden, the host's antioxidant systems are activated to cope with the stress and attempt to restore redox balance via compensatory mechanisms. In other words, despite a general depletion of the thiol pool, the preservation of thiol–disulfide transformation ratios may indicate that redox homeostasis is still being maintained (Erel and Erdogan 2020).

Plasma proteins, particularly albumin and globulin, are important biomarkers during infectious processes and may exhibit divergent changes during the APPs. Albumin, the most abundant protein synthesized by the liver, plays critical roles in maintaining oncotic pressure, transporting various molecules, supporting tissue repair, preserving redox balance, and contributing to antioxidant defense (Fitri et al. 2016). It is classified as a major negative APPs, and its serum levels typically decline during APPs (Cray et al. 2009). This decrease may result from reduced hepatic synthesis, transcapillary leakage, malnutrition, or the redirection of amino acid pools toward the production of positive APPs (O'Sullivan et al. 2016). Globulin levels are associated with immune activation and antibody production and may increase or decrease depending on the infection stage (Lawal et al. 2024). In the present study, no statistically significant differences were observed in serum albumin, globulin, or total protein levels between *Plasmodium*-infected geese and uninfected geese. These findings suggest that the infection had not yet induced a systemic disruption in protein metabolism or that the host organism was able to compensate through homeostatic mechanisms. Moreover, the biochemical response to infection in this case appeared to be primarily shaped by inflammation and oxidative stress, evidenced by elevated SAA, Hp, and TSA levels and decreased thiol concentrations—rather than by the total protein alterations typically observed in later stages of APPs (Cray et al. 2009; Bozukluhan and Merhan 2023). Taken together, these observations allow us to interprete that the infection may be

in a subclinical phase, in which systemic protein metabolism remains relatively stable, while acute phase and redox-related pathways are preferentially engaged (Cray et al. 2009). This interpretation is supported by the concordant acute phase protein and thiol–disulfide homeostasis findings, although it should be considered cautiously in the absence of longitudinal data.

In this study, correlation and PCA provide further insight into the integrated biochemical response to *Plasmodium* infection in geese. In particular, the relationships observed between APPs and TDH parameters suggest that *Plasmodium* infection triggers oxidative stress and that the increase in Hp levels reflects a close interplay between inflammatory activation and thiol-based antioxidant defense mechanisms. Moreover, the associations among TDH parameters indicate that a coordinated redox response is regulated during infection (Murata et al. 2004; Pesti-Asbóth et al. 2023). Multivariate analysis further supports this interpretation, as the principal component discriminating infected and uninfected geese is mainly driven by protein-related and thiol-based redox parameters. Collectively, these findings indicate that infection-associated biochemical alterations are primarily reflected in inflammatory and oxidative stress-related pathways rather than in marked disruptions of serum protein homeostasis (Faraguna et al. 2025).

Conclusion

This study shows that *Plasmodium* infection in geese is associated with pronounced inflammatory responses and alterations in oxidative stress-related parameters, as reflected by higher acute phase protein levels and lower thiol-based antioxidant concentrations (TT, NT, and DS). Notably, the stability of thiol–disulfide ratios and the absence of significant changes in albumin, globulin, and total protein concentrations suggest that host regulatory mechanisms remain active and may contribute to maintaining systemic homeostasis under moderate biochemical stress. The combined evaluation of all analyses indicates that infection-related biochemical alterations occur in a coordinated manner, with protein-related and thiol-based redox parameters contributing to the differentiation between infected and uninfected geese. These findings suggest that the infection did not induce marked alterations in serum protein fractions, which may reflect a subclinical infection and the activation of homeostatic mechanisms maintaining protein balance, consistent with the non-specific nature of the acute phase response. APPs and TDH parameters therefore appear to have potential as integrated biomarkers for enhancing the biochemical characterization of avian malaria and for monitoring systemic responses associated with infection. Future studies should investigate the temporal dynamics of these biomarkers throughout the course of infection and assess their behavior in response to antiparasitic treatment.

Limitations and future directions

This study presents important and original findings by elucidating biochemical responses in domestic geese naturally infected with *Plasmodium* under field conditions; however, several limitations should be considered. First, the cross-sectional design of the study precludes causal inferences regarding the observed associations between infection status and biochemical parameters. Because the analyses were conducted at a single time point, interpretation of temporal changes in biomarkers throughout the course of infection is limited. In the absence of longitudinal data, it is not possible to clearly determine when these biochemical alterations begin or whether they resolve, persist, or worsen during disease progression or potential recovery. In addition, the absence of serological data (e.g., antibody titers) prevented discrimination between recent and long-standing infections, thereby limiting interpretation of infection timing and prior immune exposure. This limitation is particularly relevant for the assessment of infections with limited or subtle systemic responses, which may not be fully captured by single-time-point measurements. Second, although TDH and APPs were comprehensively evaluated, other cellular antioxidant defense mechanisms, such as superoxide dismutase, catalase, and glutathione peroxidase, as well as markers of oxidative damage, including lipid peroxidation products and protein carbonyls, were not analyzed. Inclusion of these parameters could have contributed to a more comprehensive assessment of redox imbalance and cellular damage. Although no significant changes were observed in total serum protein levels, the lack of subclass-specific immunoglobulin analyses may have limited a more detailed understanding of the immunological nuances of the host response. In addition, sampling was performed during a single seasonal period, which restricted evaluation of the potential effects of seasonal variation in vector activity on infection intensity and host responses. Furthermore, the study population consisted exclusively of female geese within a relatively narrow age range. As inflammatory, oxidative, and protein-related physiological parameters are known to vary according to sex and age, this should be considered when interpreting the findings. Finally, the study included only naturally infected domestic geese from a limited geographic region, which constrains the generalizability of the findings to other avian species and ecological conditions. Therefore, future studies using experimental infection models and comparative approaches across different bird species, sexes, and age classes are warranted. Future research should aim to (i) monitor biomarkers at multiple time points during infection and recovery in geese from different regions, (ii) evaluate the temporal

dynamics and reversibility of changes in TDH and APPs, and (iii) investigate the effects of antiparasitic treatments on these biochemical parameters. Such studies will contribute to a better understanding of host–parasite interactions and support the development of diagnostic and therapeutic strategies for monitoring avian *Plasmodium* spp. infections.

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Data Availability The data supporting the findings of this study are included within the article.

Declarations

Conflict of interest The authors report there are no competing interests to declare.

Ethical approval All procedures involving animals were approved by the Kafkas University Local Ethics Committee for Animal Experiments (Approval No.: 2015/067) and were conducted in accordance with national and institutional guidelines.

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