UNIVERSIDADE ESTADUAL DE SANTA CRUZ

GLEICIELLE RODRIGUES MOTA

HIERARQUIA DE DOMINÂNCIA EM ARTIODÁCTILOS: FATORES SOCIAIS E FISIOLÓGICOS

ILHÉUS-BAHIA

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Tese apresentada ao Programa de Pós-graduação em Ciência Animal da Universidade Estadual de Santa Cruz como parte dos requisitos para obtenção do título de doutor em Ciência Animal.
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Em memória de José de Oliveira Mota.

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RESUMO

Esta tese investiga a hierarquia de dominância em mamíferos por meio de dois capítulos: o primeiro apresenta uma revisão de escopo da literatura existente, enquanto o segundo consiste em um estudo experimental com caititus (*Dicotyles tajacu*). No primeiro capítulo, foi conduzida uma revisão sobre as evidências acumuladas sobre a hierarquia de dominância em ungulados, com base em publicações indexadas nas bases de *dados Web of Science* e *Scopus*. O principal objetivo foi analisar as variáveis testadas e os métodos empregados para avaliar e classificar os animais dentro da hierarquia de dominância. Os resultados indicam que a escolha do método de avaliação pode impactar significativamente as conclusões, uma vez que diferentes abordagens variam em sensibilidade e são influenciadas pela falta de observações entre díades. Além disso, destaca-se a importância das hipóteses relacionadas aos atributos individuais e à dinâmica social na explicação da formação das hierarquias, sugerindo que fatores intrínsecos e extrínsecos interagem para determinar o posicionamento dos indivíduos. O segundo capítulo apresenta um estudo experimental cujo o objetivo foi avaliar relação entre as posições dos indivíduos em redes sociais de interações agonísticas e afiliativas e seus níveis de estresse, avaliados por meio da concentração de metabólitos de glicocorticoides nas fezes. Foi testada a hipótese de que os indivíduos mais dominantes ocupariam posições centrais tanto nas redes sociais agonísticas quanto nas afiliativas, sendo seu papel central crucial para prevenir a escalada da agressão entre os indivíduos, facilitando assim a integração de fêmeas aparentadas e machos não aparentados. O experimento foi conduzido com três grupos de caititus mantidos em cativeiro. Os resultados revelam que, em um dos grupos, a hierarquia de dominância se mostrou quase linear, com indivíduos mais centrais nas redes agonísticas sendo também os mais dominantes e pesados. No entanto, não foi observada correlação entre a centralidade nas redes sociais (agonísticas ou afiliativas) e os níveis de glicocorticoides. A ausência de uma hierarquia linear nos outros dois grupos corroboram com estudos anteriores que apontam para a flexibilidade na estrutura social dos caititus. Assim, esta tese contribui para a compreensão da complexidade das hierarquias de dominância, ressaltando a influência de fatores metodológicos e contextuais na análise das dinâmicas sociais em caititus

Palavras-chave: estrutura social, metabólitos de glicocorticoides, pecaris, rank de dominância, rede social.

ABSTRACT

This thesis investigates dominance hierarchy in mammals through two chapters: the first presents a scoping review of the existing literature, while the second consists of an experimental study with collared peccaries (*Dicotyles tajacu*). In the first chapter, a review of the accumulated evidence on dominance hierarchy in ungulates was conducted, based on publications indexed in the Web of Science and Scopus databases. The main objective was to analyze the tested variables and the methods used to assess and classify animals within the dominance hierarchy. The results indicate that the choice of evaluation method can significantly impact conclusions, as different approaches vary in sensitivity and are influenced by the lack of observations between dyads. Additionally, the importance of hypotheses related to individual attributes and social dynamics in explaining the formation of hierarchies is highlighted, suggesting that intrinsic and extrinsic factors interact to determine individual positioning. The review also emphasizes the need for further research in still underexplored areas. The second chapter presents an experimental study examining the relationship between individuals' positions in social networks of agonistic and affiliative interactions and their stress levels, assessed through fecal glucocorticoid metabolite concentrations. The experiment was conducted with three groups of captive collared peccaries. The results reveal that, in one of the groups, the dominance hierarchy was nearly linear, with more central individuals in the agonistic networks also being the most dominant and heaviest. However, no correlation was observed between centrality in social networks (agonistic or affiliative) and glucocorticoid levels. The absence of a linear hierarchy in the other two groups supports previous studies pointing to the flexibility of collared peccary social structure. Thus, this thesis contributes to understanding the complexity of dominance hierarchies, highlighting the influence of methodological and contextual factors in analyzing social dynamics in artiodactyls.

Keywords: Social structure, Glucocorticoid Metabolites, Social Network, Peccaries, Dominance Rank.

Sumário

1 INTRODUÇÃO GERAL

Em grupos pequenos e estáveis, os indivíduos ajustam suas interações de acordo com o contexto e a identidade dos membros do grupo com quem interagem (Romero et al., 2009; Wilson et al., 2013). Esses ajustes influenciam a frequência das interações e a preferência por determinados indivíduos, permitindo compreender seu impacto na coesão do grupo (Aureli & Schino, 2019). Um dos aspectos mais relevantes para a manutenção da coesão social é a estrutura do grupo, ou seja, a organização das relações entre os indivíduos, frequentemente expressa por uma hierarquia de dominância, característica presente em diversas espécies de animais (Shizuka & McDonald, 2012; Strauss et al., 2022). A hierarquia de dominância pode ser definida como uma assimetria nos comportamentos agonísticos, incluindo agressões, deslocamentos espaciais, submissão e evitação entre indivíduos (Drews, 1993). Quando as relações de dominância e submissão estão bem estabelecidas, a hierarquia de dominância é considerada estável (Kravitz & Huber, 2003). Nessas condições, os confrontos físicos são raros e as disputas por recursos ocorrem, predominantemente, por meio de comportamentos simbólicos de dominância e submissão. Esse mecanismo reduz o risco de ferimentos e minimiza a dispersão dos indivíduos subordinados, promovendo a estabilidade do grupo (Chase et al., 2002; King & Sueur, 2011).

As interações sociais são moldadas por fatores intrínsecos e extrínsecos ao indivíduo, influenciando a estrutura social como um todo (Chase et al., 2002). Um exemplo disso é a associação entre o peso e o ranking de dominância, em que indivíduos mais pesados tendem a ser mais dominantes (Ergül Ekiz et al., 2020; Górecki & Dziwińska, 2014; Sánchez-Dávila et al., 2018). Compreender como essa rede de interações conecta os indivíduos em um grupo é essencial para explicar os padrões de organização social (Godde et al., 2013).

Na hierarquia de dominância, por exemplo, essa rede é formada por interações agonísticas, que incluem comportamentos como ameaças e fugas, os quais determinam a posição dos indivíduos na hierarquia (Hinde, 1976). Já os comportamentos afiliativos, relacionados à cooperação e ao suporte social, variam conforme a posição do indivíduo na hierarquia. Indivíduos dominantes, por exemplo, podem ocupar posições centrais nas redes de interações afiliativas (Brent et al., 2011). Além dos diferentes tipos de interação, existem diversos métodos de análise e índices que quantificam essas interações sociais (Balasubramaniam et al., 2013; Farine & Whitehead, 2015). A escolha do método de

avaliação é crucial para determinar a associação entre variáveis, como por exemplo, a relação entre o ranking de dominância e os níveis de glicocorticoides, frequentemente associados ao estresse social (Sapolsky et al., 2000).

De modo geral, os indivíduos podem ajustar suas interações com diferentes membros do grupo de acordo com sua posição na hierarquia de dominância (Schino, 2007). Esse grau de diferenciação entre os animais aumenta a complexidade da rede social, uma vez que exige o reconhecimento das posições relativas na hierarquia dos membros do grupo (Lazzaroni et al., 2017). Indivíduos dominantes podem apresentar mais ou menos interações afiliativas em comparação com os subordinados. Em lobos (*Canis lupus arctos*), por exemplo, observou-se uma redução na agressão após interações amigáveis entre o agressor e o receptor da agressão (Lazzaroni et al., 2017). Sugere-se que isso ocorra devido aos níveis elevados de estresse vivenciados pelos oponentes após um conflito, tanto pelo efeito da agressão em si quanto pelo risco de novos ataques, o que motivaria a expressão de comportamentos afiliativos como forma de reduzir o estresse (Wu, 2021). Tais comportamentos teriam a função de reparar relações rompidas e diminuir o risco de novas agressões (Romero et al., 2009). Dessa forma, avaliar a rede social de animais mantidos em cativeiro permite identificar como as interações afiliativas e agonísticas são distribuídas entre os indivíduos, bem como a relação entre essas interações e o estresse provocado por conflitos sociais (Abbott et al., 2003).

A secreção de glicocorticoides (GCs: cortisol e corticosterona) é uma resposta endócrina clássica ao estresse (Sapolsky et al., 2000). Atualmente, esses hormônios são os biomarcadores mais utilizados para avaliar a resposta fisiológica a situações estressantes (Botía et al., 2023). A relação entre interações sociais e a função do eixo HPA (hipotálamo-pituitária-adrenal) é bem estabelecida em primatas (Brent et al., 2011; Romero et al., 2009; Sapolsky, 2005; Sapolsky et al., 2000). Em primatas não humanos, por exemplo, a posição do animal na hierarquia de dominância está frequentemente associada aos níveis de cortisol, com indivíduos subordinados apresentando concentrações mais elevadas de GCs em comparação com os dominantes (Abbott et al., 2003). No entanto, Wooddell e colaboradores (2017) não encontraram relação entre os níveis de GCs e a agressão em macacos Rhesus. Uma possível explicação é que indivíduos que recebem altas taxas de agressão, comum em sociedades despóticas como a dessa espécie, são capazes de prever a agressão antes que ela ocorra. A previsibilidade tem sido associada a níveis reduzidos de cortisol (Agrigoroaei et al., 2013). Além disso, como mencionado anteriormente, a reconciliação após interações agressivas pode ajudar

a mitigar a resposta do eixo HPA (Romero et al., 2009). No mesmo estudo, Wooddell e colaboradores (2017) observaram que indivíduos que iniciavam interações sociais afiliativas com maior frequência apresentavam menor atividade do eixo HPA. Esses achados sugerem que a agressão, por si só, pode não ser suficiente para explicar a atividade do eixo HPA, uma vez que os indivíduos podem lidar com o estresse por meio de outros mecanismos (Wooddell et al., 2017). Como, por exemplo, o apoio social e o reforço de laços afiliativos. Interações afiliativas, como o grooming e a proximidade social, podem atuar como moduladores da resposta ao estresse, promovendo a redução dos níveis de GCs e auxiliando na homeostase fisiológica (Silk et al., 2010).

Diante disso, esta tese tem como objetivo explorar como as redes de interações sociais e, em particular, a hierarquia de dominância impactam o estresse fisiológico dos animais, utilizando como modelo o caititu (*Dicotyles tajacu*). A tese foi dividida em dois capítulos. No primeiro, realizou-se uma revisão de escopo da literatura sobre os fatores associados ao ranking de dominância em espécies de artiodátilos. O segundo capítulo aborda a organização social dos caititus sob cuidados humanos, investigando a conexão entre as redes sociais, a hierarquia de dominância e o estresse fisiológico. O caititu é um mamífero neotropical encontrado desde a América do Norte até a América do Sul (Fragoso, 1998). Seus grupos variam em tamanho, coesão e estrutura social (Byers & Bekoff, 1981). A espécie exibe uma estrutura social que ainda necessita de estudos mais aprofundados. Por exemplo, enquanto alguns estudos descrevem a estrutura social dos caititus como uma hierarquia linear de dominância, outros sugerem relações de dominância circulares, indicando a falta de consenso sobre uma estrutura linear clara (da Silva et al., 2016; Faria et al., 2022; Nogueira-Filho et al., 1999).

2 OBJETIVO GERAL

Este estudo visa descrever e analisar a hierarquia de dominância social em espécies de ungulados e caititus (Dicotyles tajacu) mantidos sob cuidados humanos, investigando as relações entre dominância, fatores sociais e fisiológicos, e os métodos de análise utilizados. Além disso, o estudo busca aplicar e validar esse conhecimento no manejo de animais em ambientes artificiais, considerando suas redes de interações sociais e os impactos sobre o estresse fisiológico.

2.1 OBJETIVOS ESPECÍFICOS

No primeiro capítulo, os objetivos foram: 1. levantar a literatura científica existente sobre os fatores que influenciam e são influenciados pelo ranking de dominância em ungulados, tanto em animais de vida livre quanto em animais mantidos em ambientes artificiais, considerando aspectos físicos, fisiológicos e sociais. 2. Analisar as metodologias utilizadas para investigar a estrutura social de ungulados e classificar os indivíduos em um ranking de dominância, destacando suas limitações e potenciais metodológicos. 3. Identificar os principais objetivos dos estudos sobre hierarquia de dominância, diferenciando abordagens em animais de vida livre (condições naturais) e em animais mantidos em cativeiro (condições artificiais). No segundo capítulo, foitestada a seguinte hipótese: indivíduos mais dominantes ocupariam posições centrais tanto em redes sociais agonísticas quanto afiliativas, com seu papel central sendo crucial para prevenir a escalada de agressão entre os indivíduos, facilitando assim a integração de fêmeas relacionadas e machos não relacionados.

3 REVISÃO DA LITERATURA

3.1 INTRODUÇÃO

A complexa rede de relações sociais entre os animais tem sido objeto de estudo de diversos pesquisadores ao longo dos anos (Bernstein, 1981; Farine & Whitehead, 2015; Pasquaretta et al., 2014; Strauss et al., 2022; Strauss & Holekamp, 2019). Quando

dois indivíduos interagem repetidamente, cada interação pode influenciar as subsequentes, construindo uma história única que define sua relação social (Schino, 2007). Essas interações, frequentemente moldadas por diversos fatores, desempenham um papel fundamental na estrutura social do grupo como um todo (Aureli & Schino, 2019). As observações de Schjelderup-Ebbe em 1922 sobre a assimetria nas agressões entre galinhas deram origem a uma das publicações mais influentes no estudo do comportamento animal. O conceito de "ordem hierárquica" foi rapidamente aplicado a outras espécies (Strauss et al., 2022) e, desde então, tornou-se um dos temas mais estudados na ecologia comportamental, sendo ainda investigado mais de cem anos após sua formulação (Hobson, 2022).

A hierarquia de dominância emerge e persiste em diversos grupos taxonômicos, incluindo aves (French & Smith, 2005), peixes (Chase, 1980) e mamíferos (Muller & Wrangham, 2004). As diferenças no status de dominância influenciam diretamente as chances de sobrevivência dos indivíduos, determinando o acesso a recursos essenciais, como alimento (Taillon & Côté, 2007), território e parceiros reprodutivos (Espmark, 1964). Embora a manutenção da dominância tenha um custo energético elevado, esse esforço pode ser compensado pelo acesso prioritário a recursos, resultando em maior massa corporal, taxa de crescimento e saúde física, culminando em um maior sucesso reprodutivo (Taillon & Côté, 2007). Por outro lado, para os subordinados, evitar interações agressivas com indivíduos mais dominantes pode ser uma estratégia para garantir sua permanência no grupo (Simons et al., 2022).

.3.2 Atributos Prévios

Quando dois indivíduos se confrontam, ambos avaliam a capacidade de luta do oponente em relação à sua própria para determinar a reação mais apropriada (Chase et al., 2002; Setchell et al., 2008). Essa avaliação é conhecida como a hipótese dos "atributos prévios", que sugere que as hierarquias de dominância lineares são formadas com base em características dos indivíduos que indicam seu potencial para reter recursos (Chase et al., 2002). Entre esses atributos estão massa corporal, idade, personalidade, perfil hormonal e condições físicas. Em primatas não humanos, por exemplo, indivíduos mais pesados tendem a ser mais dominantes (Zhang et al., 2021). Esse padrão também é observado em algumas aves (French & Smith, 2005) e ungulados (Grossel et al., 2022). Em outras espécies, a coloração ou estruturas físicas podem estar associadas à dominância. Por exemplo, Setchell e Wickings (2005) observaram que a submissão unidirecional é mais comum entre machos de mandril (*Mandrillus sphinx*) quando há uma

diferença evidente na coloração, enquanto ameaças e agressões ocorrem com mais frequência entre machos de coloração semelhante. Esses sinais de status são utilizados para minimizar conflitos durante o estabelecimento da dominância e frequentemente estão correlacionados ao ranking social (Strauss & Shizuka, 2022).

3.3 Dinâmica Social

Outra hipótese que busca explicar a linearidade nas hierarquias de dominância está relacionada aos processos de interação social entre os membros do grupo, conhecida como a hipótese da dinâmica social (Chase et al., 2002). Fatores como o efeito vencedor-perdedor desempenham um papel crucial na manutenção dessas hierarquias (Chase, 1980). Esse efeito refere-se ao fato de que indivíduos que vencem uma disputa aumentam sua probabilidade de vencer disputas futuras, enquanto perdedores aumentam sua probabilidade de perder as disputas subsequentes (Parker, 1974). Além disso, o efeito de observadores, onde indivíduos ajustam seu comportamento com base na observação de encontros agonísticos de outros, também é relevante (Drews, 1993).

De acordo com a hipótese da dinâmica social, se as interações sociais não ocorressem no contexto do grupo, as hierarquias não desenvolveriam suas estruturas lineares usuais (Strauss et al., 2022). Assim, as hierarquias de dominância seriam vistas como sistemas auto-organizados, cujas estruturas gerais são determinadas pela interação entre os elementos que compõem o sistema (Aureli & Schino, 2019). Algumas espécies, por exemplo, combinam informações sociais para fazer inferências sobre a capacidade de luta de um indivíduo, sem a necessidade de observar diretamente todas as disputas (Strauss & Shizuka, 2022). Essa inferência transitiva baseia-se na dedução lógica de que, se o indivíduo A domina B e B domina C, então A domina C, mesmo que A e C não tenham disputado diretamente (De Vries, 1998).

3.4 Métodos de Análise Hierárquica e Classificação em um *Ranking* de Dominância

A análise da hierarquia de dominância tem como objetivo descrever a estrutura social de um grupo, que pode ser linear ou despótica (De Vries, 1998). Em uma hierarquia linear, a relação de dominância é transitiva, o que significa que, para qualquer tríade de indivíduos A, B e C no grupo, a condição "se A domina B e B domina C, então A também domina C" deve ser verdadeira. Landau (1951) e Kendall (1962) desenvolveram um

índice de linearidade, chamado índice h, que expressa a força da linearidade presente em um conjunto de relações de dominância. Um valor de 1,0 para o índice h indica linearidade completa, enquanto um valor de 0,0 sugere que cada indivíduo domina um número igual de outros indivíduos (de Vries et al., 2006).

3.4.1 - Indice h’

Posteriormente, De Vries (1998) propôs o índice de linearidade h', uma versão corrigida do índice h de Landau, ajustada para o número de interações desconhecidas. Quando a linearidade em um conjunto de relações de dominância é significativamente maior do que o esperado pelo acaso, os indivíduos podem ser ordenados em uma hierarquia de dominância linear ou quase linear. O cálculo do índice de linearidade h' ocorre em duas etapas. Na primeira etapa, atribui-se uma pontuação às células da matriz de dados, com base na proporção de vitórias e derrotas dos indivíduos em interações com outros membros do grupo. Para díades sem interações observadas (díades nulas), a pontuação é atribuída com base na proporção de vitórias e derrotas desses indivíduos em disputas com outros membros do grupo. Em seguida, calcula-se a medida de linearidade, que fornece uma avaliação inicial da estrutura hierárquica presente nos dados. Na segunda etapa, todas as relações de dominância-submissão entre os pares são aleatorizadas, realizando-se 10.000 aleatorizações. Esse processo permite comparar a linearidade da matriz observada com a linearidade esperada, avaliando se a estrutura hierárquica observada é resultado do acaso ou reflete um padrão significativo (de Vries, 1998).

3.4.3 Escore de David

Um índice amplamente utilizado para avaliar a dominância é o escore de David, que se baseia em uma matriz de ganhador/perdedor (De Vries, 1998). Esse método tem sido amplamente aplicado para descrever a estrutura social de diversas espécies (Neumann & Fischer, 2023). Para calcular a dominância, cada indivíduo recebe uma pontuação com base no sucesso total em relação a todos os outros membros do grupo. Essa pontuação é determinada subtraindo a soma ponderada e não ponderada das proporções de vitórias e derrotas de um indivíduo em cada díade (de Vries, 1998). A pontuação normalizada de David corrige a probabilidade de interações ocorridas ao acaso e é ajustada ao número de indivíduos no grupo, tornando-se mais robusta à medida que o número de interações aumenta. Por isso, a pontuação normalizada de David é recomendada para calcular um valor estável e confiável de dominância, especialmente

em situações com poucas mudanças ao longo do tempo (Hoppitt & Farine, 2018; Sánchez-Tójar et al., 2018).

3.4.4 *Elo-rating* e *Elo-rating* Aleatorizado

O Elo-rating, amplamente utilizado em esportes como o xadrez, ganhou popularidade no estudo do comportamento animal devido à sua capacidade de acompanhar a dinâmica da dominância ao longo do tempo (Neumann & Kulik, 2014). No entanto, o Elo-rating padrão apresenta limitações, como o viés da ordem em que as interações ocorrem, o que pode distorcer a interpretação da linearidade na hierarquia (Sánchez-Tójar et al., 2018). Por outro lado, o Elo-rating randomizado aplica o mesmo princípio do Elo-rating, mas aleatoriza a sequência das interações, permitindo que esse processo seja repetido várias vezes para gerar uma média das posições hierárquicas dos indivíduos (Neumann & Fischer, 2023; Sánchez-Tójar et al., 2018). Esse método é particularmente recomendado para grupos cujos tamanhos e composições variam ao longo do tempo, pois oferece uma avaliação mais robusta e menos influenciada pela ordem das interações.

3.4.5 Análises de redes sociais

A transitividade de triângulos, proposta por Shizuka e McDonald (2012), é um índice baseado na enumeração direta das tríades em redes sociais, sem inferir valores para díades nulas. Esse método utiliza matrizes de dominância, em que a relação de dominância e submissão é representada por arestas direcionadas do nó dominante ao submisso. Quando dois indivíduos vencem o mesmo número de disputas, ambos recebem a mesma pontuação, e díades mútuas (empates) são consideradas raras no estudo da dominância (Shizuka & McDonald, 2012). Essas díades são vistas como estados transitórios, pois ocorrem apenas quando os integrantes da díade interagem um número par de vezes (McDonald & Shizuka, 2013). Do ponto de vista metodológico, díades mútuas e díades nulas são semelhantes, já que ambas representam uma relação não resolvida entre os indivíduos (Neumann et al., 2018). Por isso, é essencial considerar tanto as interações existentes quanto as ausentes na análise de redes de dominância (Shizuka & McDonald, 2012).

Para avaliar a significância do método, utiliza-se uma abordagem semelhante à de De Vries (1995), mas com uma diferença crucial: não há imputação de dados para díades nulas. Na teoria das redes, emprega-se a abordagem de gráfico uniforme condicional, que consiste em gerar 1.000 grafos aleatórios (Wasserman & Faust, 1994). Esses grafos

simulam a estrutura de dominância para grupos hipotéticos com o mesmo número de indivíduos e o mesmo número de relações de dominância observadas na rede empírica. No entanto, diferem na distribuição das relações de dominância: em vez de replicar as relações exatas observadas, cada indivíduo tem a mesma probabilidade de dominar qualquer outro na rede. Em seguida, os valores de transitividade dos triângulos nessas redes aleatórias são comparados com o valor empírico de transitividade. Essa comparação permite determinar se a transitividade observada na rede real é significativamente maior do que o esperado pelo acaso em uma rede onde as relações de dominância são distribuídas de forma uniforme entre os indivíduos (Shizuka & McDonald, 2012).

A relação de dominância é apenas uma das possíveis interações entre dois indivíduos. Nesse contexto, as análises de redes sociais permitem avaliar as relações entre indivíduos de forma mais abrangente, utilizando ferramentas matemáticas (Farine & Whitehead, 2015). Entre essas ferramentas, destacam-se: Coeficiente de centralidade do autovetor: Considera não apenas a força e o número de conexões de um indivíduo, mas também a centralidade dos indivíduos aos quais ele está conectado (Krause et al., 2007). Coeficiente de centralidade de intermediação: Mede o número de caminhos mais curtos que passam por um indivíduo, indicando seu grau de influência sobre o fluxo de informações ou interações na rede (Wilson et al., 2013). Coeficiente de agrupamento: Avalia o quanto os indivíduos tendem a se agrupar com outros, o que pode indicar a estabilidade do grupo. Um coeficiente de agrupamento elevado sugere que o grupo é mais sensível à remoção de determinados indivíduos (King & Sueur, 2011).

4 ANIMAIS ESTUDADOS

Os artiodáctilos são mamíferos naturalmente distribuídos em todas as regiões, exceto na Antártida e Austrália, com muitas espécies introduzidas em áreas não nativas (Solari & Baker, 2007). Essa ordem apresenta uma notável diversidade em tamanho corporal, morfologia, adaptações alimentares e tolerância ambiental (Gatesy et al., 1999; Hassanin et al., 2011). Destaca-se por incluir a maioria dos mamíferos herbívoros

domesticados, como gado, renas, camelos, porcos, cabras e ovelhas (Solari & Baker, 2007).

Análises moleculares e genéticas confirmaram uma estreita relação evolutiva entre os cetáceos (Ordem Cetacea) e os hipopótamos, levando à proposta de uma classificação revisada que integra esses grupos (Montgelard et al., 1997). Alguns pesquisadores sugeriram renomear a ordem como Cetartiodactyla para refletir essa relação evolutiva, enquanto outros defendem a manutenção da classificação tradicional, posicionando Artiodactyla e Cetacea em uma categoria taxonômica superior, sob a mesma superordem (Hassanin et al., 2011). No presente estudo optou-se por utilizar a denominação ungulados como referências a todos os artiodáctilos terrestres.

Atualmente, os ungulados estão agrupados em 10 famílias: Bovidae, a mais diversificada, com 142 espécies; Cervidae, que inclui veados e alces, totalizando 54 espécies; Moschidae, que compreende os cervos-almiscarados, com 7 espécies; Giraffidae, que inclui girafas e okapis; Antilocapridae, representada pelo antilocapra, com apenas 1 espécie; Tragulidae, que inclui os tragulídeos, com 10 espécies; Hippopotamidae, que inclui os hipopótamos, com 2 espécies; e Camelidae, que inclui camelos, dromedários, lhamas, com 7 espécies; Suidae, que compreende os porcos, com 18 espécies; Tayassuidae, que inclui os pecaris, com 3 espécies.

O caititu (*Dicotyles tajacu* Linnaeus, 1758), espécie estudada no segundo capítulo desta tese, é um mamífero neotropical que pertencente à família Tayassuidae (Figura 1). Esta espécie pode viver em grupos compostos por machos e fêmeas em igual proporção, além de seus filhotes, e que podem atingir até 50 indivíduos (Sowls, 1978). Esses grupos são coesos e habitam diversos tipos de habitats, desde a América do Norte até a América do Sul (Fragoso, 1998). Esta espécie não é considerada ameaçada de extinção na maior parte de sua área de distribuição, sendo classificada como menos preocupante segundo a União Internacional para Conservação da Natureza (IUCN) (Gongora et al., 2011). Entretanto, é considerada extinta em alguns locais (Reyna-Hurtado et al., 2017). Entre as ameaças que a espécie enfrenta, além da perda de habitat, destaca-se a caça de subsistência (Gongora et al., 2011). Por isso, a criação desses animais têm sido apontada como uma alternativa à caça de subsistência (Nogueira Filho & Nogueira, 2000). Além de serem mantidos em confinamento para fins de produção, também são usados para fins de educação ambiental e recreação em zoológicos de diversos países (Faria et al., 2022).

A espécie destaca-se por exibir repertório comportamental vasto e interações interindividuais complexas, que ainda precisam ser melhor estudadas (Bonnemaison et

al., 2021). Alguns estudos foram feitos com o intuito de compreender o comportamento de defesa e social da espécie (Bonnemaison et al., 2021; Nogueira et al., 2007, 2017), além de avaliar o bem-estar dessa espécie quando mantido sob cuidados humanos (Nogueira et al., 2011; Faria, et al., 2022). Sobre a estrutura social, não existe consenso. Em alguns estudos, uma única hierarquia de dominância linear, que incluiria tanto machos quanto fêmeas, descreveria a estrutura social dos grupos de caititus (Silva et al., 2016b; Dubost, 2000). Porém, outro estudo descreveu relações de dominância circulares entre indivíduos, o que não tornaria possível descrever uma estrutura de dominância linear para os grupos dessa espécie (Nogueira-Filho et al., 1999).

Em relação a avaliação das redes sociais, Biondo e colaboradores (2014) verificaram a correlação positiva entre o parentesco e a coesão do grupo de caititus mantidos sob cuidados humanos. Neste mesmo trabalho, também foi observado que os indivíduos mais jovens ocupam uma posição mais central nas redes de interações sociais devido a maior tolerância dos adultos em relação aos juvenis (Biondo et al., 2014). Essas diferenças mostram que, embora essa espécie seja altamente social, a interação entre membros do grupo é variável, de modo que mudanças como a retirada ou adição de indivíduos pode ter efeitos muito diferentes na estrutura social como um todo.

Figura 1 - Grupo de caititus mantidos nas dependências do Laboratório de Etologia Aplicada da Universidade Estadual de Santa Cruz-UESC.

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6. CAPÍTULO 1

Social Dominance Hierarchy in Artiodactyls: A Scoping Review of Influencing Factors and Methods

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Abstract

This review examines the current state of research on dominance hierarchies in wild and captive ungulates, focusing on the factors influencing and being influenced by dominance rank. A total of 120 studies, encompassing 37 species from nine families, were analyzed. The review reveals an increase in research since the early 2000s, with studies predominantly conducted in artificial conditions. The most frequently studied factors include physical traits such as body mass, aggressiveness, and age. Despite the use of various ranking methods, including index-based approaches, there is considerable variation in the methodologies employed across studies, which calls for greater standardization. The review also identifies gaps in the literature, particularly in terms of underrepresented species and the integration of environmental, social, and physiological factors into dominance research. Overall, this review provides a comprehensive overview of current methodologies and highlights the need for further research to advance our understanding of dominance hierarchies in ungulates.

Keywords: Dominance hierarchy, ungulates, ranking methods, social dynamics.

1. Introduction

Artiodactyls, also known as ungulates, form a diverse group of mammals that include both wild and domesticated species (Prothero, 2007). Wild species inhabit various ecosystems, from forests to grasslands (Rose, 1996), while domesticated species have been selectively bred and adapted to human-managed environments (Solari & Baker, 2007). A characteristic of ungulates is the formation of social groups (Prothero, 2007). Social animals adjust their interactions according to context and the identity of their partners (Aureli & Schino, 2019), influencing interaction frequency and individual preferences within the group, which plays a role in maintaining cohesion (Clutton-Brock & Huchard, 2013). A crucial aspect of group cohesion is its social structure, often expressed through dominance hierarchies, which are present across various species (Shizuka & McDonald, 2012; Strauss et al., 2022).

A dominance hierarchy is defined as a pattern of repeated agonistic interactions between individuals, where outcomes consistently favor one member of the dyad, leading to submissive responses instead of escalating aggression (Drews, 1993). Rank indicates an individual's relative position within the hierarchy based on interactions among all group members (Bernstein, 1981). In linear hierarchies, dominance relationships follow a transitive pattern: if individual A dominates B, and B dominates C, then A also dominates C. Non-linear hierarchies, in contrast, contain intransitive triads where A dominates B, B dominates C, but C dominates A, indicating a less rigid and more egalitarian social organization (Albers & De Vries, 2001; Schmid & De Vries, 2013). Linear hierarchies, observed in many social species, reduce uncertainties in social interactions, promoting greater stability (Chase et al., 2002; Strauss et al., 2022). Conversely, non-linear hierarchies, characterized by intransitive relationships, may increase competition and conflict (Strauss & Shizuka, 2022), potentially affecting group cohesion and management in captive (Sosa et al., 2019).

Understanding social interactions among animals is crucial for measuring dominance hierarchies (Levy et al., 2020a). Researchers classify dominance using ordinal or cardinal metrics. Ordinal metrics assign each individual a position within the hierarchy based on simple ranking (e.g., 1 to n) or proportional rank, which accounts for group size (Levy et al., 2020a). Cardinal metrics, on the other hand, determine rank order and quantify the magnitude of differences between adjacent individuals. Additionally, individuals ranked using these metrics may be categorized into broader classifications such as low, medium, and high ranking, or subordinate, intermediate, and

dominant. However, the choice of ranking metric is often made without explicitly acknowledging its underlying assumptions (Levy et al., 2020b). This decision is critical, as different metrics may yield varying results when predicting dominance-related traits (Balasubramaniam et al., 2013).

Choosing an appropriate methodological approach is essential for understanding how individual characteristics (pre-existing attributes) and social interactions contribute to hierarchy formation and rank establishment (Grossel et al., 2022). The prior attributes hypothesis suggests that hierarchies form based on inherent individual traits that determine dominance potential, such as age, sex, body size (mass, height, or width), and the size of morphological structures like horns and antlers (Palaoro & Peixoto, 2022). Physiological factors, including hormone levels (Brent et al., 2011), and temperament traits like aggressiveness, also play a role (Colléter & Brown, 2011). In contrast, the social dynamics hypothesis posits that dominance hierarchies emerge from interactions among group members rather than being predetermined by individual attributes (Chase et al., 2002). Mechanisms such as the winner-loser effect, where initial victories or defeats influence future contest outcomes, and the bystander effect, where individuals adjust behavior after observing third-party interactions, are key drivers of hierarchy formation (Chase, 1980).

In natural environments, dominance hierarchies are influenced by ecological factors, particularly resource availability (Wittemyer & Getz, 2007). In contrast, captivity imposes artificial conditions such as restricted space and controlled feeding, which can alter social dynamics, increasing aggression and hierarchy instability (Houpt & Wolski, 1980). While stable hierarchies in natural settings promote group cohesion by minimizing conflicts and facilitating cooperative behaviors (Keiper & Sambraus, 1986), instability in captive groups can lead to stress, increased aggression, and social disruptions. Understanding dominance structures is therefore essential for refining management strategies in captive populations (Brouns & Edwards, 1994). For instance, in captive breeding programs, introducing new individuals should consider social ranking to prevent imbalances and aggression (Fraser, 2008).

Despite extensive research on dominance hierarchies, significant gaps remain. One major limitation is the lack of standardization in ranking methodologies, making comparisons across studies challenging. Additionally, integrating environmental, social, and physiological factors remains complex. Addressing these gaps requires a more holistic approach to studying social structures in ungulates. This review aims to evaluate

the species studied and methodologies used to investigate social structures by using factors influencing dominance rank in wild and captive ungulates, considering physical, physiological, and social aspects.

2. Material and Methods

For this review, scientific articles were collected from the *Scopus and Web of Science* databases, both of which are multidisciplinary platforms that enable systematic searches with precision, transparency, and reproducibility (Gusenbauer & Haddaway, 2020). We tested multiple search strings and selected the one that included the highest number of references to artiodactyls. The final search string was "Dominance AND Hierarchy OR Dominance AND Rank," which initially returned 1,678 journal articles (hereafter referred to as reports). All identified articles were retrieved and assessed for eligibility. This screening process was conducted manually by two reviewers for each article (a flow diagram detailing the retrieval process is provided in Figure 1).

The article search was conducted in February 2024, with newly published studies continuously added until July 30. Reports that did not meet the inclusion criteria (Table 1) were subsequently excluded. After these exclusions, 120 reports remained, and data were extracted from each text.

First, key objective variables were summarized, including authors' names, journal names, year of publication, country where the study was conducted, species studied, and testing conditions (natural or artificial settings). Following, articles were categorized more precisely based on predefined definitions and criteria established before the literature search (Table 1, Supplementary Material). After summarizing the literature, we analyzed sample size (number of animals), sex, taxa examined, testing conditions, ranking methods, and factors related to physical, physiological, ecological, and social aspects. Additionally, we compiled the types of variables correlated with an animal's position in the dominance rank and organized them by condition.

To determine whether there was a difference in the proportion of natural vs. artificial testing conditions in the reports, we performed a chi-square test. The Wilcoxon test was used to compare the distributions of samples from two independent groups without assuming normality in the data distributions. In this case, the natural and artificial conditions. Following the Wilcoxon test, we calculated the rank-biserial correlation (r), an effect size measure that quantifies the magnitude of the difference

between the two groups in terms of the ranks of the sample values. A Wilcoxon test was also conducted to compare the average observation time per animal between two distinct conditions. Spearman's rank correlation was used to assess the relationship between the observation time per individual and the number of interactions collected.

For all analyses, the significance level was $\alpha \leq 0.05$. A contingency matrix is used to graphically depict the relationships between the factors associated with the dominance rank using Igraph package (Csardi & Nepusz, 2006). All analyses were performed using R software, version 4.3.3 (R Core Team, 2024).

Table 1 - Methodological parameters extracted from each article identified in the review process.

Parameter	Description
Species	Species analyzed in each study (ungulates), organized according to their respective taxonomic families.
Number of Animals	Total number of individuals used in each article, specifying the total per studied group.
Sex	Quantification of the number of males and females used in each article.
Number of Groups	Number of social groups analyzed in each study.
Number of Dyadic Interactions	Total number of recorded dominance and submission interactions between pairs of individuals (dyads), used for classifying animals into dominance rankings.
Type of experimental conditions	Natural: Studies conducted in the species' natural geographic distribution, without significant experimental manipulation (e.g., no space or resource limitations). Artificial: Studies conducted in manipulated environments (e.g. zoos) or with experimentally altered groups. Artificial: Studies conducted in restricted environments or where the group was experimentally manipulated regarding sex, number of individuals.
Study Duration	Total observation time in each study, specified in hours.
Country	Country where the primary data were collected. Specify whether the study took place in protected areas, conservation sites, or experimental facilities.

Data Collection Method	Methods used to record social interactions, such as focal animal sampling, scan sampling, or others.
Classification type	Ordinal: Numerical values to individuals according to their position within a hierarchy, ranging from the highest (rank 1) to the lowest (rank n, where n represents the total number of individuals in the hierarchy). Cardinal: Proportion of wins and losses in agonistic encounters between dyads. Categorical: categorical classification of rank in low-meddle-high ranking or subordinate-intermediary-dominant.
Classification Method	Mathematical or statistical methods used to establish dominance rankings. Examples include: David's Score, Elo-rating, I&SI, Beilharz index, Clutton-Brock index, among others.
Type of Covariate Related to Ranking	Parameters correlated with the dominance ranking, related to prior attributes (e.g., sex, age, weight) or social dynamics (e.g., frequency of affiliative or agonistic interactions).
Year	Year of publication.

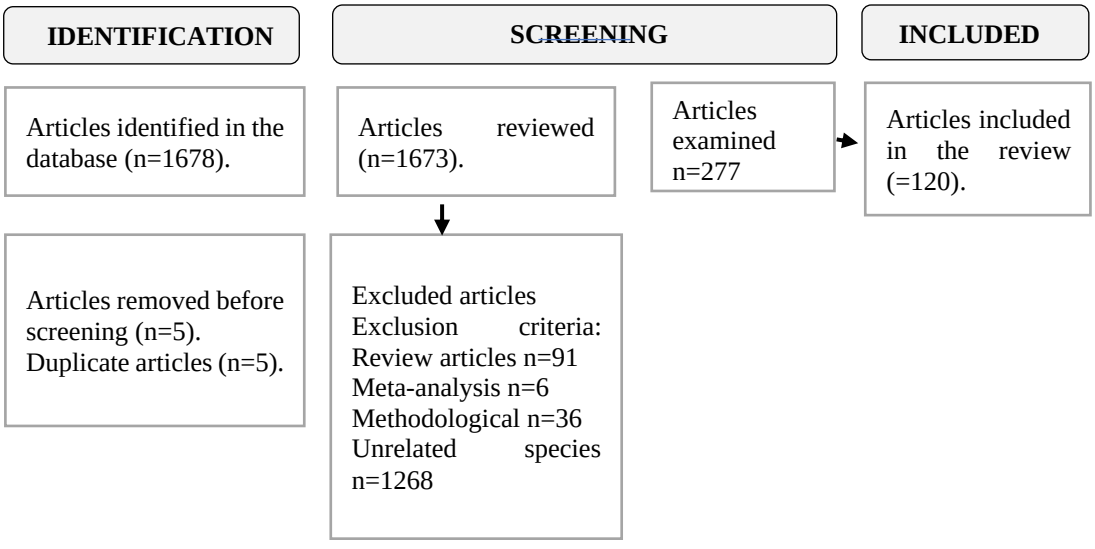

Figure 1- Literature Search Flow Diagram: Displays the number of studies identified, retained, and excluded at each stage of the review process.

3. Results

Our search yielded 1678 initial results, of which 120 met the eligibility criteria and were included in this review for further assessment. The oldest record was from 1964 (Figure 2a). A total of 37 species, including subspecies, belonging to nine families were identified (Figure 2b). The highest number of reports belong to the family Bovidae (53), followed by Cervidae (20), Suidae (17), Equidae (16), Elephantidae (6), Tayassuidae (4), Giraffidae (2), Camelidae (1), and Moschidae (1). The three most studied species were *Bos taurus* (21 reports), *Sus scrofa* (17 reports), and *Equus caballus* (11 reports). The full list of species, as well as their respective families, can be found in Table 2.

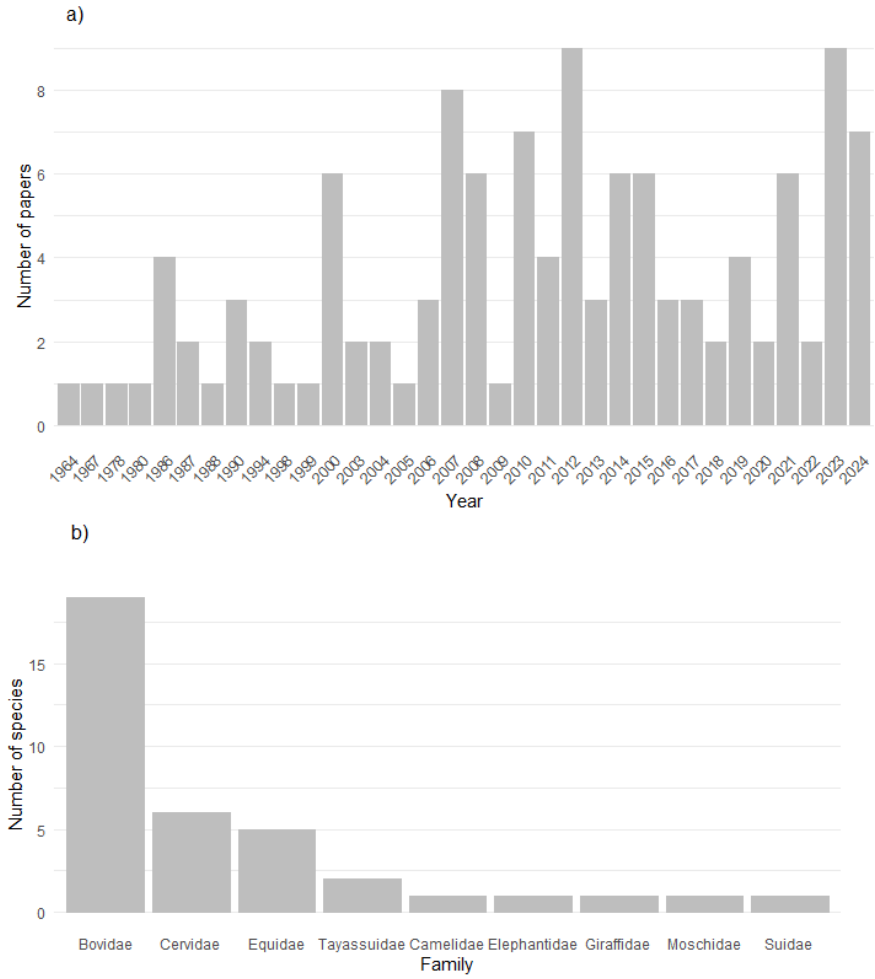

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Figure 2- Studies on social dominance hierarchy in ungulates. (a) Number of articles published over the years. (b) Number of species studied by taxonomic family.

176 Table 2- Summary of species and subspecies reviewed, showing the distribution of

177 reported by country and experimental conditions

Family	Specie	Country	type of condition	Report
Bovidae	*Aurotragus derbianus*	Senegal	Natural	Vymyslicka 2015
Bovidae	*Ammotragus lervia*	Spain	Artificial	Cassinello & Calabuig 2008
Bovidae	*Alcelaphus buselaphus*	Georgia	Artificial	Spratt et al., 2019
Bovidae	*Bison bison*	Belgium	Artificial	Vervaecke et al., 2005
Bovidae	*Bison bison bison*	United_States	Natural	Mooring et al., 2006
Bovidae	*Bos indicus*	Brazil	Artificial	Soares-Valente et al., 2023
Bovidae	*Bos taurus*	Brazil	Artificial	Coimbra et al., 2012
Bovidae	*Bos taurus*	Brazil	Artificial	Bica et al., 2019
Bovidae	*Bos taurus*	Brazil	Artificial	Pinheiro et al., 2020
Bovidae	*Bos taurus*	Brazil	Artificial	Gorecki et al., 2021
Bovidae	*Bos taurus*	Canada	Artificial	Val-Laillet et al., 2008
Bovidae	*Bos taurus*	Canada	Artificial	Fories et al., 2021
Bovidae	*Bos taurus*	Canada	Artificial	Kondo & Hurnik 1990
Bovidae	*Bos taurus*	China	Artificial	Hodgson et al., 2024
Bovidae	*Bos taurus*	Czech_Republic	Artificial	Sarova 2010
Bovidae	*Bos taurus*	Czech_Republic	Artificial	Sarova 2013
Bovidae	*Bos taurus*	Czech_Republic	Artificial	Sarova et al., 2016
Bovidae	*Bos taurus*	France	Artificial	Soffie & Zayan 1978
Bovidae	*Bos taurus*	France	Artificial	Ramseyer et al., 2009
Bovidae	*Bos taurus*	Germany	Artificial	Reinhardt et al., 1986
Bovidae	*Bos taurus*	Germany	Artificial	Hohenbrink & Meinecke 2012
Bovidae	*Bos taurus*	Italy	Artificial	Canali et al., 1986
Bovidae	*Bos taurus*	Italy	Artificial	Bagnato et al., 2023
Bovidae	*Bos taurus*	United_States	Artificial	Dickson et al., 1967
Bovidae	*Bos taurus*	United_States	Artificial	Harris et al., 2007
Bovidae	*Bos taurus*	United_States	Artificial	Bruno et al., 2017
Bovidae	*Bos taurus*	Uruguay	Artificial	Fiol et al., 2019
Bovidae	*Bubalus bubalis*	Brazil	Artificial	Madella-Oliveira et al., 2012
Bovidae	*Capra aegagrus hircus*	Mexico	Artificial	Sanchez-Davila et al. 2018
Bovidae	*Capra aegagrus hircus*	Spain	Artificial	Barroso et al., 2000
Bovidae	*Capra aegagrus hircus*	Turkey	Artificial	Tolu & Savas 2007
Bovidae	*Capra aegagrus hircus*	United_States	Artificial	King et al., 2019
Bovidae	*Capra ibex*	Switzerland	Natural	Willisch & Neuhaus 2011
Bovidae	*Capra ibex nubiana*	Israel	Natural	Greenbergcohen et al., 1994
Cervidae	*Capreolus capreolus*	France	Natural	Maublanc et al., 1987
Cervidae	*Cervus elaphus*	Czech_Republic	Artificial	Dusek et al., 2007
Cervidae	*Cervus elaphus*	Czech_Republic	Artificial	Bartos et al., 2010
Cervidae	*Cervus elaphus*	Czech_Republic	Artificial	Nemeth et al., 2021
Cervidae	*Cervus elaphus*	Scotland	Natural	Schmidt et al., 1998
Cervidae	*Cervus elaphus*	Spain	Artificial	Perez-Barberia et al., 2021

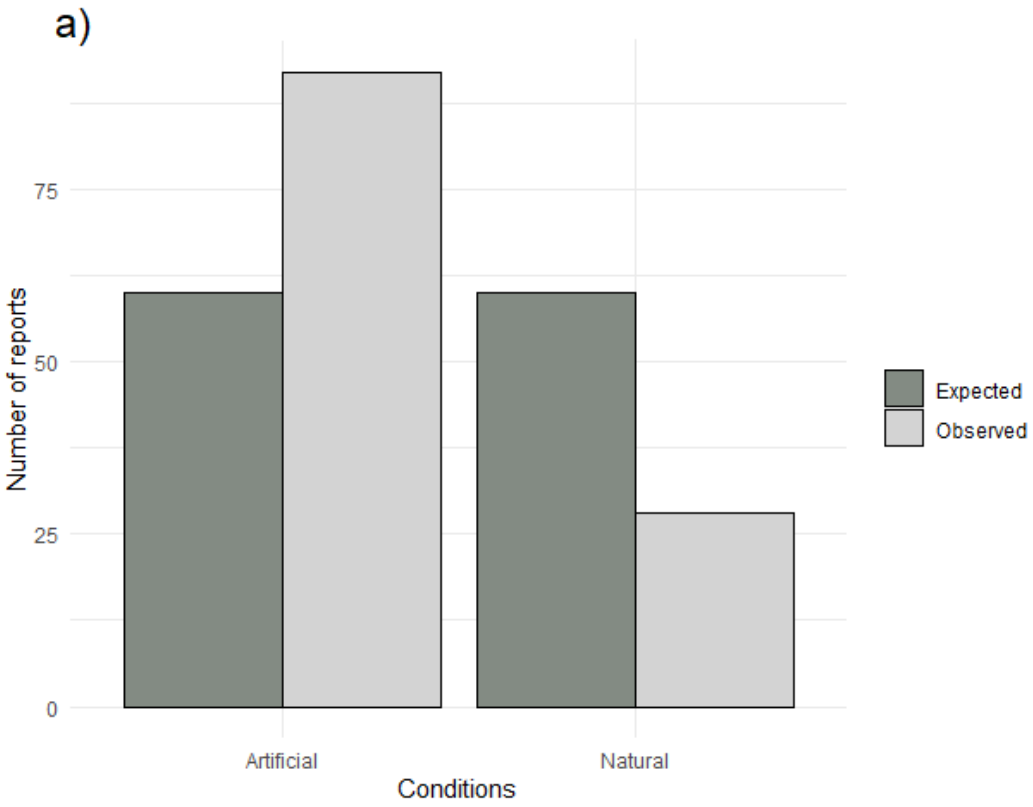
Cervidae	*Dama dama*	Ireland	Natural	Jennings et al., 2010
Cervidae	*Dama dama*	Ireland	Natural	Jennings et al., 2011
Cervidae	*Dama dama*	Ireland	Natural	Bateman-Neubert et al., 2023
Tayassuidae	*Dicotyles tajacu*	Brazil	Artificial	da Silva et al., 2016
Equidae	*Equus caballus*	Belgium	Artificial	Haag et al., 1980
Equidae	*Equus caballus*	Canada	Artificial	Taillon & Cotê 2008
Equidae	*Equus caballus*	Czech_Republic	Artificial	Komarkova et al., 014
Equidae	*Equus caballus*	England	Artificial	Giles et al., 2015
Equidae	*Equus caballus*	France	Artificial	Briard et al., 2015
Equidae	*Equus caballus*	Georgia	Artificial	Weeks et al., 2000
Equidae	*Equus caballus*	Germany	Artificial	Krueger & Heinze 2008
Equidae	*Equus caballus*	Iceland	Artificial	Sigurjonsdotti et al., 2003
Equidae	*Equus caballus*	Italy	Natural	Schneider & Krueger 2012
Equidae	*Equus caballus*	Portugal	Artificial	Heitor & Vicente 2010
Equidae	*Equus caballus*	United_States	Natural	Rutberg & Greenberg 1990
Equidae	*Equus ferus*	Switzerland	Artificial	Freymond et al., 2013
Equidae	*Equus ferus caballus*	Italy	Natural	Krueger et al., 2014
Equidae	*Equus ferus przewalskii*	Germany	Artificial	Keiper & Sambraus 1986
Equidae	*Equus ferus przewalskii*	Mongolia	Natural	Bernatkova et al., 2023
Equidae	*Equus ferus przewalskii*	United_States	Natural	Keiper 1988
Equidae	*Equus quagga*	Uganda	Natural	Fugazzola 2012
Bovidae	*Gazella dama mhorr*	Spain	Artificial	Cassinello_2000
Bovidae	*Gazella dorcas neglecta*	Spain	Artificial	Cortes et al., 2024
Giraffidae	*Giraffa camelopardalis*	Czech_Republic	Artificial	Horova et al., 2015
Giraffidae	*Giraffa camelopardalis*	Japan	Artificial	Saito et al., 2023
Camelidae	*Lama guanicoe*	Chile	Artificial	Correa et al., 2013
Elephantidae	*Loxodonta africana*	Kenya	Natural	Wittemyer 2007
Elephantidae	*Loxodonta africana*	Kenya	Natural	Wittemyer et al., 2007
Elephantidae	*Loxodonta africana*	Namibia	Natural	Oconnell-Rodwell et al., 2011
Elephantidae	*Loxodonta africana*	United_States	Artificial	Freernan 2010
Elephantidae	*Loxodonta africana*	United_States	Artificial	Leighty 2010
Elephantidae	*Loxodonta africana*	United_States	Artificial	Mouttham 2011
Moschidae	*Moschus chrysogaster*	China	Artificial	Wang 2024
Cervidae	*Odocoileus virginianus*	Canada	Artificial	Taillon & Cotê 2006
Cervidae	*Odocoileus virginianus*	Canada	Artificial	Taillon & Cotê 2007
Bovidae	*Oreamnos americanu*	Canada	Natural	Hamel 2008
Bovidae	*Oreamnos americanus*	Canada	Natural	Taillon & Cotê 2006
Bovidae	*Oreamnos americanus*	Canada	Natural	Cote 2000
Bovidae	*Ovis aries*	Australia	Artificial	Sherwin & Johnson 1987
Bovidae	*Ovis aries*	Greece	Artificial	Lee & Kim 2022
Bovidae	*Ovis aries*	Greece	Artificial	Papadaki et al., 2024
Bovidae	*Ovis aries*	Mexico	Artificial	Aguirre et al., 2007
Bovidae	*Ovis aries*	Mexico	Artificial	Veliz-Deras et al., 2022
Bovidae	*Ovis aries*	Poland	Artificial	Gorecki & Dziwinska 2014

Bovidae	*Ovis aries*	Turkey	Artificial	Ergul et al., 2020
Bovidae	*Ovis aries*	United_Kingdom	Artificial	Hewitson et al., 2007
Bovidae	*Ovis aries*	United_Kingdom	Natural	Briefer et al., 2015
Bovidae	*Ovis canadensis*	Canada	Natural	Pelletier & Festa-Bianchet 2006
Bovidae	*Ovis gmelini*	France	Artificial	Guilhem et al., 2000
Cervidae	*Ozotoceros bezoarticus*	Poland	Artificial	Ungerfeld & Freitas-de-Melo 2014
Cervidae	*Ozotoceros bezoarticus*	Uruguay	Artificial	Morales-Pineyrua et al 2014
Cervidae	*Ozotoceros bezoarticus*	Uruguay	Artificial	Ungerfeld et al., 2015
Cervidae	*Ozotoceros bezoarticus*	Uruguay	Artificial	Villagran 2018
Cervidae	*Rangifer tarandus*	Canada	Natural	Barrette & Vandal 1986
Cervidae	*Rangifer tarandus*	Finland	Natural	Hirotani 1990
Cervidae	*Rangifer tarandus*	Finland	Artificial	Holand et al 2004
Cervidae	*Rangifer tarandus*	Sweden	Artificial	Espmark 1964
Suidae	*Sus scrofa*	Australia	Artificial	Greenwood et al., 2017
Suidae	*Sus scrofa*	Austria	Artificial	Veit 2024
Suidae	*Sus scrofa*	Canada	Artificial	Warns et al., 2021
Suidae	*Sus scrofa*	France	Artificial	Parois et al., 2017
Suidae	*Sus scrofa*	Germany	Artificial	Hoy et al., 2008
Suidae	*Sus scrofa*	Germany	Artificial	Manteuffel 2010
Suidae	*Sus scrofa*	Germany	Artificial	Schamun 2012
Suidae	*Sus scrofa*	Germany	Artificial	Fels et al., 2012
Suidae	*Sus scrofa*	Germany	Artificial	Lagoda et al., 2021
Suidae	*Sus scrofa*	Hungary	Artificial	Ujvary 2012
Suidae	*Sus scrofa*	United_Kingdom	Artificial	Oconnell et al., 1999
Suidae	*Sus scrofa*	Spain	Artificial	Oliveira et al., 2023
Suidae	*Sus scrofa*	Spain	Artificial	Ochoteco-Asensio et al., 2024
Suidae	*Sus scrofa*	United_Kingdom	Artificial	Brouns & Edwards 1994
Suidae	*Sus scrofa*	United_Kingdom	Artificial	Litten et al., 2003
Suidae	*Sus scrofa*	United_States	Artificial	Horback & Parsons 2016
Suidae	*Sus scrofa*	United_States	Artificial	Sommer et al., 2023
Bovidae	*Taurotragus oryx*	Czech_Republic	Artificial	Musa et al., 2024
Bovidae	*Taurotragus oryx*	United_States	Artificial	Wirtu et al., 2004
Tayassuidae	*Tayassu pecari*	Brazil	Artificial	Nogueira et al., 2012
Tayassuidae	*Tayassu pecari*	Brazil	Artificial	Alencar et al., 2023
Tayassuidae	*Tayassu pecari*	Brazil	Artificial	Vieira et al., 2023

3.1 Differences in study frequency and observation time between natural and artificial conditions

The number of studies conducted in artificial conditions was higher compared to those in natural (N=120, $\chi^2 = 34.13$, $df = 1$, $p < 0.001$; Figure 3a). The value of the rank-biserial correlation (r) was -0.31. The value of r = -0.31 indicates a moderate difference between the two groups, with a tendency for the artificial group to have larger sample sizes than the natural group. This value also indicates that although the difference is significant, the effect size is moderate. (Figure 3b). On average, the number of groups studied per report was 5 in artificial environments and 2 in natural environments.

The difference in average observation time (hours per individual) between the two conditions is not significant (N= 19, W = 25, $p = 0.95$). For the artificial condition, the mean time was 22.08h (SE= 3.58), while for the natural condition, the mean time was 11.77h (SE = 2.96). No significant relationship was observed between the observation time and the number of interactions collected in either the natural (rho = 0.50, p>0,05) or artificial (rho= -0.43, p>0,05) conditions.



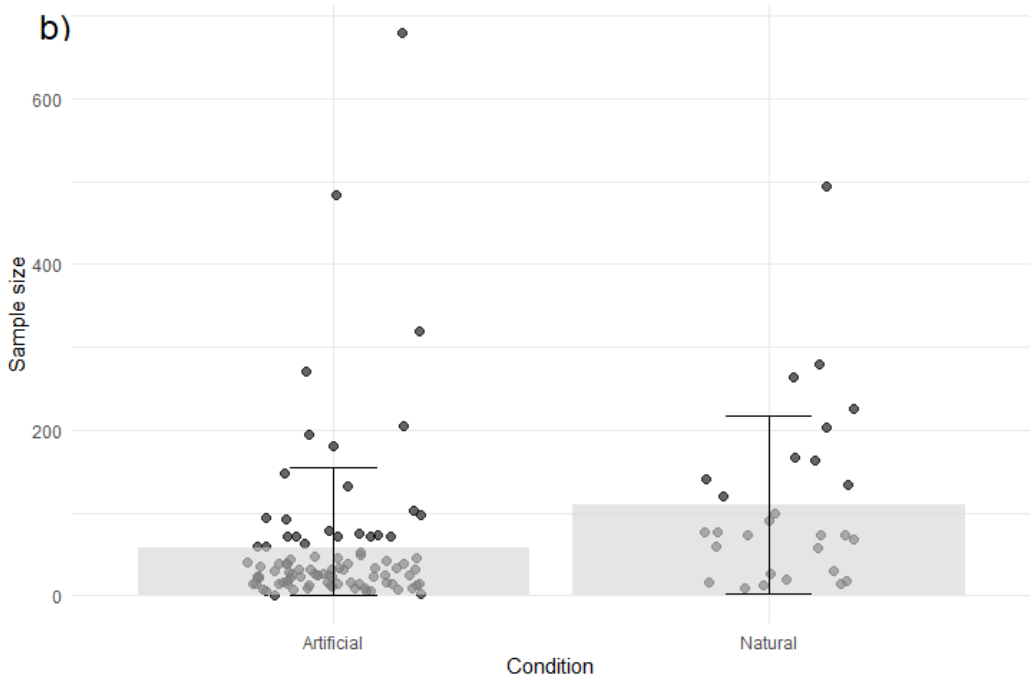


Figure 3- a) Comparison of the number of studies conducted in artificial versus natural conditions b) sample sizes between studies conducted in artificial and natural conditions.

3.2 Key factors influencing dominance rank in natural and artificial conditions

The most frequently studied factors among the reports on artificial conditions include physical factors such body mass (29 reports), followed by consumption rate (16), and aggressiveness (14). In natural conditions, age (8) body mass (7) and aggressiveness (5) was the most frequently studied factors among the reports (Table 4 supplementary material). Body mass (weight) is also a central variable with connections to age, aggressiveness, horn size, and consumption rate (Figure 4).

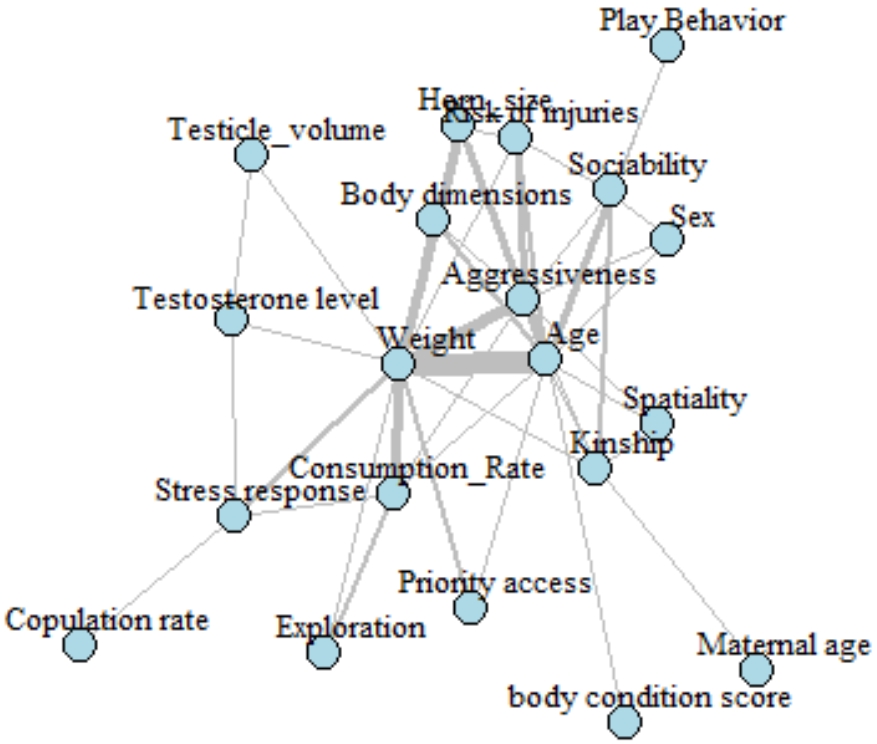


Figure 4- Graphical representation of the associations between variables identified in the reports (more than one). The line thickness reflects the frequency of associations, with thicker lines indicating more frequent associations and thinner lines indicating less frequent ones.

3.3 Classification and Methodological Approaches in Dominance Ranking Studies

The results indicate that ordinal classification is the most commonly used approach in the analyzed studies with 54 occurrences (45%), while categorical and cardinal classifications are equally frequent with 33 reports (27.5%) each. Although index-based methods are the most frequently used in dominance ranking studies, they exhibit considerable variation in the type of calculation applied. A total of 28 reports from different indices were found, with the most frequently cited being the I&SI index (DeVries, 1998), the David score (David, 1963), ADI (Hemelrijk et al., 2005), and the Clutton-Brock index (1979).

4. Discussion

The review highlights trends and gaps in the study of dominance hierarchies in ungulates, shedding light on both the methodologies used and the factors that influence social dynamics in wild and captive environments. Despite notable progress in the field, certain challenges persist, particularly in standardizing ranking methodologies and integrating multifaceted factors that influence dominance hierarchies. These factors include physical, physiological, and social variables, which are crucial for understanding the complexities of dominance interactions within different species.

There is a substantial increase in publications on dominance hierarchies since the early 2000s. The same pattern was found by Hobson et al. (2022), signaling a growing interest in this area of research. However, the fact that a higher proportion of studies are conducted in artificial conditions compared to natural environments raises concerns about the ecological validity of dominance assessments and their applicability to wild species, which are subject to more complex social and environmental pressures (Clutton-Brock & Huchard, 2013).

Studies on wild species (e.g., *Ozotoceros bezoarticus*, *Tayassu pecary*, *Dicotyles tajacu*, *Odocoileus virginianus*) have occurred at a lower frequency compared to studies on domesticated species (*Sus scrofa*, *Bos taurus*, *Equus caballus*, *Ovis aries*). For conservation purposes, understanding dominance structures in free-ranging species is crucial, as they can influence resource access, reproductive success, and overall population dynamics (Taillon & Cotê 2006). For example, in caribou (*Rangifer tarandus caribou*), dominant individuals, particularly adult females with larger antlers, have better access to food craters, which are essential for survival during winter (Barrette and Vandal, 1986). Similarly, in elephants (*Loxodonta africana*), dominant groups occupy preferred habitats and avoid high-risk areas, reducing energy expenditure and predation risk during the dry season (Wittemyer et al., 2007a).

Dominance hierarchies contribute to social stability by reducing conflicts and establishing predictable access to resources. In Przewalski's horses (*Equus ferus przewalskii*), linear dominance hierarchies reduce aggression and promote group cohesion, which is essential for survival in harsh environments (Keiper, 1988). Similarly, in reindeer (*Rangifer tarandus*), dominance hierarchies based on body weight maintain social stability, even in temporary groups (Hirotani, 1990). Conservation efforts should aim to preserve the social structures of these species, as disruptions to

dominance hierarchies can lead to increased aggression, reduced group cohesion, and lower survival rates.

In general body mass and age are often positively correlated with dominance, as larger and older individuals tend to have competitive advantages in agonistic interactions (Brouns & Edwards, 1994; da Silva et al., 2016; Hirotani, 1990; Weeks et al., 2000). Aggressiveness can reinforce dominance status by facilitating priority access to food and mates (Esattore et al., 2021), although excessive aggression may increase social stress and negatively impact group cohesion. Sociability, on the other hand, can mitigate the costs of competition by promoting affiliative interactions and reducing conflict frequency (Warns et al., 2021). Feeding rate is also frequently linked to body mass and age, with dominant individuals typically exhibiting higher consumption rates due to their priority access to resources (Brajon et al., 2021). This dominance-related advantage in food intake can lead to greater weight gain and improved production performance in livestock species.

Ecological factors play a crucial role in shaping dominance hierarchies, influencing both individual access to resources and the dynamics of social interactions. In the studies reviewed, the spatial distribution of foraging areas and resource availability was found to significantly affect dominance rankings, with individuals in environments where resources were clumped or limited tending to dominate feeding sites, reinforcing hierarchical structures (Wittemyer & Getz, 2007). In contrast, study conducted in with abundant resources suggested that dominance rank played a less pronounced role, as the widespread availability of food minimized direct competition (Schmidt et al., 1998).

Habitat structure cam be important determinant of dominance expression, with open environments facilitating overt aggression and visual displays of power however, no studies were found that evaluate this relationship. Seasonal and climatic factors also appeared to impact dominance rank, with studies noting that during resource scarcity, dominance hierarchies became more pronounced, as individuals competed more intensely for limited resources (Barrette & Vandal, 1986). Reproductive state was another factor influencing dominance patterns, with dominant individuals often gaining priority access to mates during breeding seasons (Barrette & Vandal, 1986; Espmark, 1964). These findings underscore the importance of considering ecological contexts when interpreting dominance hierarchies, as habitat conditions, resource distribution,

and environmental stressors can all contribute to the variability in dominance structures across species and environments.

Dominance ranks are established based on the outcomes of dyadic agonistic interactions between individual (Drews, 1993). Agonistic interactions are recorded *ad libitum* during daily data collection, typically conducted alongside randomized focal animal sampling and scan samples, except to classification based on body trait like horn size (Schmidt et al., 1998). The significant difference in sample sizes between artificial and natural conditions, with larger sample sizes typically observed in artificial settings, was expected, given that most studies are conducted on domesticated species. However, the effect of sample size is not particularly large, which may indicate that, in natural conditions, studies tend to be conducted on groups with a high number of individuals, although the number of groups examined is lower compared to studies conducted in artificial environments. This pattern suggests that while field studies may include fewer independent groups, they still provide robust insights into social structures within larger group. The lack of significant difference in observation time between natural and artificial conditions indicates that methodological approaches in both settings may be comparable in terms of data collection efforts.

Ordinal classification remains the most commonly employed approach. Index-based methods such as the I&SI index, the David score, ADI, and the Clutton-Brock index are the most used. Although these indices are frequently cited, they often differ in how dominance is calculated (Neumann et al., 2018), which may lead to inconsistencies across studies (Sánchez-Tójar et al., 2018). This variation complicates direct comparisons between studies conducted in artificial and natural conditions or even between studies at similar conditions, further emphasizing the need to standardize ranking methods and develop a unified framework as discussed by levy et al. (2020). Standardization would not only facilitate cross-study comparisons but also improve the reliability of dominance assessments in both conservation and experimental research contexts (Levy, et al., 2020).

Simple ordinal ranks are generated by assigning numbers to individuals based on their position in the hierarchy, from the highest (rank 1) to the lowest (rank n, where n is the total number of individuals in the hierarchy). For example, the top-ranking individual in a group would be given a rank of 1, the second would be 2, and so on. In contrast, cardinal rank takes into account the number of individuals in the hierarchy(Levy, Gesquiere, et al., 2020; Levy, Zipple, et al., 2020). It measures the

proportion of individuals in the hierarchy that an individual outranks. This means that instead of just assigning a position based on order, proportional rank expresses how an individual compares to others in terms of the percentage of the hierarchy they outrank(Neumann et al., 2011). Categorical rank is a way of grouping individuals into broad categories based on their position in the hierarchy, such as "low," "middle," or "high" ranking, rather than assigning a specific numeric rank. These categories are typically defined by breaking the hierarchy into ranges or quantiles.

Different indices have been used across studies to classify individuals into both ordinal and categorical rankings(Balasubramaniam et al., 2013). Furthermore, the categorization method, such as dominant-subordinate or low-middle-high ranking, does not follow specific criteria and is typically carried out subjectively by the authors. Unlike ordinal rank (which assigns a specific numerical value) or proportional rank (which measures an individual's position as a proportion of the entire hierarchy), categorical rank is more qualitative. It is often employed when the precise order or proportion is not as crucial for the analysis. Categorical ranking can be particularly useful when comparing groups or categories in studies where detailed ordering of individuals is less relevant.

In conclusion, the study of dominance hierarchies in ungulates reveals significant advancements and ongoing challenges. While there has been a notable increase in research, particularly in artificial environments, the ecological validity of such studies remains a concern, as they often fail to capture the complexities of wild species. The variability in ranking methodologies, including ordinal, proportional, and categorical rankings, further complicates comparisons across studies. Standardization of these methods, as proposed by previous researchers, is crucial for enhancing the consistency and reliability of dominance assessments. Additionally, the review highlights the importance of considering ecological and environmental factors in shaping dominance structures, as these factors influence not only individual behavior but also the social dynamics of species. Future research should prioritize field-based studies to better understand the natural behaviors of ungulates in wild settings, which will be essential for conservation efforts and management strategies aimed at preserving natural social structures.

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6. Supplementary Material

Table 1 - Inclusion Criteria for the Scoping Review

Criteria	Description
Social Dominance Hierarchy	Studies investigating dominance and submission relationships, considering both linear and nonlinear hierarchies and their implications for social behavior.
Dominance and Submission Relationships	Studies based on empirical observations or measurements characterizing agonistic interactions between individuals, preferably with recorded behavioral data.
Dominance Ranking	Individual classification based on agonistic encounters using the following methods: **Ordinal:** Simple ranking (e.g., 1st, 2nd, 3rd). **Cardinal:** Ranking that reflects the magnitude of differences (e.g., 1.8, 10.15, 18.5). **Categorical:** Qualitative classification (e.g., dominant-subordinate, alpha-beta-omega). Studies must provide a detailed description of the method used, including metrics such as Elo rating or David's Score, or others.
Prior Attributes	Inherent factors of individuals, including genetically determined characteristics (e.g., sex, weight, age) and other documented physical or behavioral traits that may influence dominance.
Social Dynamics	Analysis of interactions among group members, including affiliative and agonistic interactions and their effects on hierarchical structure and group stability.
Target Species	Terrestrial ungulate mammals (artiodactyls), considering studies of both captive and free-ranging groups.
Data Collection Method	Studies using direct observations, controlled experiments, or behavioral data analysis. Exclusion of purely theoretical studies or reviews without primary data collection.

Unit of Analysis	Studies analyzing social groups with a documented number of individuals.
Study condition	Studies considering groups in captivity (artificial), in the wild (natural), or both.
Methodological Quality	Inclusion of studies that provide a detailed description of the metrics used for dominance classification. Studies with insufficiently described methodology will be excluded.

Table 2-Factors correlated with dominance ranking across studies

Factors correlated to dominance ranking	**Reports**
Age	Espmark 1964, Dickson et al.,1967, Haag et al., 1980, Rreinhardt et al., 1986, Barrette & Vandal 1986, Keiper & Sambraus 1986, Keiper 1988, Rutberg & Greenberg 1990, Brouns & Edwards 1994, Cassinello & Pieters 2000, Guilhem et al., 2000, Taillon & Cotê 2006a, Taillon & Cotê 2006b, Barroso et al. 2000, Sigurjónsdóttir et al., 2003, Holand et al., 2004, Pelletier & Festa-Bianchet 2006, Wittemyer & Getz 2007, Heitor et al., 2010, Freernan et al., 2010, Nogueira et al., 2012, Ujvary et al., 2012, Sarova et al., 2013, Correa et al., 2013, Gorecki 2014, Gorecki 2014, Vymyslicka 2015, Giles et al., 2015, Horova et al., 2015, Briard ete al., 2015, da Silva et al., 2016, Gorecki et al., 2021, Bagnato et al., 2023, Alencar et al., 2023
Body mass	Espmark 1964, Dickson et al., 1967, Haag et al., 1980, Barrette & Vandal 1986, Canali et al., 1986, Hirotani 1990, Rutberg & Greenberg 1990, Brouns & Edwards 1994, Greenbergcohen et al., 1994, O'connell & Beattie 1999, Taillon & Cotê 2006b, Wirtu et al., 2004, Holand et al., 2004, Vervaeckeet al., 2005, Pelletier & Festa-Bianchet 2006, Taillon_2007b,

	Taillon et al., 2008, Heitor & Vicente 2010, Freernan et al., 2010, Bartos et al., 2010, Jennings et al., 2010, Ujvary et al., 2012, Fels 2012, Sarova et al., 2013, Gorecki & Dziwinska 2014, da Silva et al., 2016, Sanchez_Davila et al., 2018, Ergul et al., 2020, Gorecki et al., 2021, Warns et al., 2021, Veliz-Deras et al., 2022, Oliveira et al., 2023, Alencar 2023, Vieira 2023, Weeks 2000
Sex	Vymyslicka et al., 2015, Horova et al., 2015, Hodgson et al., 2024, Maublanc et al., 1987, Weeks et al., 2000
Priority access to resorse	Dickson 1967, Barrette & Vandal 1986, Sherwin & Johnson 1987, Leighty et al., 2010, Coimbra et al., 2012, Warns et al., 2021, Weeks et al., 2000
learning	Soffie & Zayan 1978, Haag et al., 1980, Manteuffel et al., 2010, Wang et al., 2024
Body dimensions	Haag et al., 1980, Taillon & Cotê 2006b, Barroso & Boza 2000, Giles et al., 2015, Ergul et al., 2020, Gorecki et al., 2021
Resource Retention	Wittemyer et al., 2007
Horn size	Barrette & Vandal 1986, Greenbergcohen et al., 1994, Cote 2000b, Barroso & Boza 2000, Holand et al., 2004, Gorecki & Dziwinska 2014, Gorecki 2021, Véliz-Deras 2022
Exploration	Canali et al., 1986, Wittemyer &Getz 2007, Freymond et al., 2013, Greenwood et al., 2017, Fiol et al., 2019, Bica et al., 2019, Ergul et al., 2020, Musa el al., 2024
Kinship	Keiper & Sambraus 1988, Guilhem et al., 2000, Taillon & Cotê 2006b, Komarkova et al., 2014, Foris et al., 2021, Weeks et al., 2000

Consumption Rate	Canali et al., 1986, Brouns & Edwards 1994, O'connell & Beattie 1999, Taillon & Cotê 2007, Taillon & Cotê 2008, Hoy et al., 2012, Madella-Oliveira et al., 2012, Ujvary et al., 2012, Greenwood et al., 2017, Fiol et al., 2019, King et al., 2019, Bica et al., 2019, Ergul et al., 2020, Oliveira et al., 2023, Sommer et al., 2023, Ochoteco-Asensio et al., 2024
Aggressiveness	Greenbergcohen et al., 1994, Schmidt et al., 1998, O'connell & Beattie 1999, Cassinell & Pieters 2000, Cote 2000b, Barroso & Boza 2000, Tolu et al. 2007, Taillon et al., 2007, Heitor et al., 2010, Jennings et al., 2010, Willisch & Neuhaus 2011, Nogueira et al., 2012, Ujvary et al., 2012, Fels et al., 2012, Correa et al., 2013, Gorecki et al., 2014, Horback & Parsons 2016, Spratt et al., 2019, Nemeth et al., 2021, Lagoda et al., 2021, Fories et. al., 2021, Bateman_Neubert et al., 2023, Wang et al., 2024, Cortes et al., 2024, Maublanc et al., 1987, Kondo & Hurnik 1990, Weeks et al., 2000
Reproductive success	Taillon & Cotê 2006, Vervaecke et al., 2005, Hoy et al., 2008, Val-Laillet et al., 2008, Greenwood et al., 2017
Maternal age	Keiper_1988, Komarkova et al., 2014
Offspring weight	Morales_Pineyrua et al., 2014, Komarkova et al., 2014
Offspring survival	Taillon & Cotê 2006, Morales_Pineyrua et al., 2014
Survival	Taillon & Cotê 2006
Spatiality	Taillon & Cotê 2006, Harris et al., 2007, Cassinello & Calabuig 2008, Ramseyer et al., 2009, Sarova et al., 2010, Horova et al., 2015, Spratt et al., 2019, Foris et al., 2021

Risk of injuries	Barroso & Boza 2000, Nogueira et al., 2012, Ujvary et al., 2012, Gorecki & Dziwinska 2014, Nemeth et al., 2021, Wang et al., 2024, Weeks et al., 2000
Growth rate	Litten et al., 2003, Vervaecke et al., 2005, Ochoteco_Asensio et al., 2024
Stress response	Mooring et al., 2006, Bartos et al., 2010, Sanchez_Davila et al., 2018, Spratt et al., 2019, Ergul et al., 2020, Oliveira et al., 2023, Saito 2023
Copulation rate	Mooring et al., 2006, Sanchez-Davila et al., 2018, Bateman-Neubert et al., 2023
Social Influence	Hewitson et al., 2007, Sarova et al., 2010, Krueger et al., 2014, Veit et al., 2024
Testosterone level	Aguirre et al., 2007, Bartos et al., 2010, O'connell-Rodwell et al., 2011, Mouttham et al., 2011, Sanchez-Davila et al., 2018, Villagran et al., 2018, Ergul et al., 2020, Soares-Valente et al., 2023
Sperm count	Villagran et al., 2018, Véliz-Deras et al., 2022
Testicle volume	Aguirre et al., 2007, Sanchez-Davila et al., 2018, Vieira 2023
Foraging Behavior	Hamel et al., 2008, Leighty et al., 2010, Sarova et al., 2010
Milk production	Dickson et al., 1967, Hohenbrink & Meinecke-Tillmann 2012
Bystander effect	Krueger et al., 2008
Intervention	Jennings et al., 2011, Schneider & Krueger 2012, Lee & Jooyoung 2022
Play Behavior	Sigurjonsdotti et al., 2003, Nogueira et al. 2012, Bagnato et al., 2023

Parasitism level	Fugazzola & Stancampiano 2012
Lameness degree	Hohenbrink & Meinecke-Tillmann 2012
body condition score	Hohenbrink & Meinecke-Tillmann 2012, Correa et al., 2013, Giles et al., 2015
Heart rate	Sigurjonsdotti et al., 2003, Briefer 2015, sommer 2023
Sociability	Keiper & Sambraus 1986, Keiper_1988, Guilhem_2000, Barroso et al., 2000, Sigurjonsdotti et al., 2003, Sarova et al., 2016, Pinheiro 2020, Fories et. al., 2021, Bagnato et al., 2023, Bernatkova et al., 2023, Musa 2024, Papadaki 2024, Hodgson et. a., 2024, Weeks 2000
Andorsterona	Parois 2017
Skin lesions	Parois 2017, Lagoda 2021, Warns 2021, Perez-Barberia et al., 2021
Shyness Boldness	Ungerfeld et al., 2014, Ungerfeld et al., 2015, Bruno et al., 2017, Oliveira et al., 2023, Briard e2015
Body temperature	Sommer et al., 2023
Vocalization	Alencar et. al 2023
Fecal microbiota	Ochoteco-Asensio et al., 2024

7. CAPÍTULO 2

Decoding dominance hierarchy and physiological stress in collared peccaries (*Dicotyles tajacu*)

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Abstract

Understanding the dynamics of dominance and social stress in group-living animals is essential for developing effective management practices. Thus, we aimed to describe the social structure of captive collared peccaries (*Dicotyles tajacu*) and discuss the possibilities and constraints of artificially arranging groups of this species. We observed social interactions in three groups of peccaries, each comprising two males and four females living in outdoor paddocks. To prevent inbreeding, males were sourced from a different origin than the females. We recorded all agonistic and affiliative interactions using a focal sampling method over 60 non-consecutive days. In addition, we collected fecal samples to measure fecal glucocorticoid metabolite (fGM) concentrations. To characterize the social structure, we used Landau's corrected linearity index (*h'*), the triangular transitivity index (t_{tri}), the directional consistency index (DCI), and hierarchy steepness. For rank determination, we employed the modified David's score (MDS), Elo rating (ER), randomized Elo rating (RER), and the improved and simplified index (I&SI). Furthermore, we computed network measures, including eigenvector centrality, density, and assortativity, from matrices of agonistic and affiliative interactions. A linear dominance hierarchy was observed in only one group (G1: h' = 0.82, p = 0.05, t_{tri} = 1.00, p = 0.01). However, the DCI and steepness across the three groups were closer to 0.0 than to 1.0, indicating potential instability in dominance relationships. Dominant individuals were central in agonistic networks across all groups when using the RER (G1: $r_{Spearman}$=0.94. p<0.01; G2: $r_{Spearman}$=0.88. p=0.01; G3: $r_{Spearman}$=0.82. p=0.04). However, they were central in affiliative networks only in G3 when using the

MDS (: $r_{Spearman}$=-0.88. p=0.01). There were positive correlations between rank and fGM concentration in two of the three groups: in G2 using the MDS ($r_{Spearman}$=0.88, p=0.01) and in G3 using the I&SI ($r_{Spearman}$=0.84, p=0.03). Additionally, there were positive correlations between rank and body weight in two of the three groups: in G2 using both the RER (G2: $r_{Spearman}$=0.82, p=0.04) and I&SI (G2: $r_{Spearman}$=0.94, p<0.01); in G1 using the MDS (G1: $r_{Spearman}$=0.88, p=0.01). These findings suggest that while dominance may influence stress in collared peccaries, further research is needed to establish causality. Although dominance relationships in captive peccaries did not follow a linear hierarchy, observed ritualistic agonistic behaviors reduced intra-group competition, preventing injuries over limited resources like food. Moreover, the results demonstrate the feasibility of introducing unfamiliar males into an established colony of related females to avoid inbreeding.

Keywords: dominance rank, hierarchy, social network, social structure, stress.

1. Introduction

In social species, dominance hierarchies often arise due to competition for resources such as food, mates, and territory (Drews, 1993). Individuals are ranked based on their ability to win conflicts or their potential to retain resources (Parker, 1974). This ranking has significant implications for physiology and animal welfare, making the study of dominance essential for understanding social dynamics and its implications for individual management (Sapolsky, 2005). The frequency of agonistic interactions among dominant individuals is influenced by the acceptance and stability of their status (Drews 1993). If widely accepted, dominant individuals engage less frequently in conflicts, leading to lower stress levels and reduced glucocorticoid concentrations, like cortisol (Colléter and Brown, 2011; Sapolsky et al., 2000). Conversely, the need to defend their status or central roles in agonistic networks may cause higher stress levels (Abbott et al., 2003). Affiliative interactions can buffer the hypothalamic-pituitary-adrenal (HPA) axis, reducing cortisol levels, as observed in chimpanzees (*Pan troglodytes*) under both acute and chronic stress (Wittig et al., 2016).

In some mammal species, social dominance is correlated with reproductive success (e.g. Muniz et al. 2010; Clutton-Brock and Huchard, 2013; Huang et al., 2024) and disease susceptibility (Sapolsky 2005; Stark et al., 2022). By examining glucocorticoid concentrations, we can understand how stress is distributed among individuals within a social group (Sapolsky et al., 2000). Elevated stress levels can lead to immune system suppression (Snyder-Mackler et al., 2020) and infertility (Tamashiro et al., 2005). In this context, the knowledge of the social structure of a species is important for a range of fundamental and applied purposes (Whitehead 2008), such as husbandry practices of captive collared peccary (*Dicotyles tajacu*).

Free-ranging collared peccaries live in relatively stable mixed-sex groups ranging from six to over 30 individuals with a 1:1 sex ratio (Gongorra et al., 2011). Group members maintain strong social ties through foraging and resting activities, indicating high cohesion (Byers and Bekoff, 1981; Ellisor and Harwell, 1969; Sowls, 1997). However, individuals may sometimes switch groups in response to changes in social dynamics, resource availability, or environmental factors (Ellisor and Harwell, 1969; Schweinsburg, 1971). Additionally, group cohesion may be disrupted during seasonal food shortages (Reyna-Hurtado et al., 2017; L. K. Sowls, 1978). This suggests that special mechanisms, such as a social structure, have evolved to promote group

cohesion (Byers and Bekoff, 1981). There is no consensus on the dominance hierarchy within this species (Biondo et al., 2014). Some studies (Byers and Bekoff, 1981; Nogueira-Filho et al., 1999) found no evidence of dominance hierarchies among peccaries, while others (Bissonette, 1982; Silva et al., 2016; Dubost, 2000) suggested that a linear dominance hierarchy characterizes the social structure of this species.

In this study, we aimed to employ complementary measurements of dominance hierarchies to better characterize and understand the social structure of collared peccary groups, as recommended by Shizuka and McDonald (2012). Furthermore, we intended to examine the relationship between stress, dominance, and the positions within affiliative and agonistic social networks. We hypothesized that more dominant individuals would occupy central positions in both agonistic and affiliative social networks, with their central role being crucial in preventing the escalation of aggression among individuals, thereby facilitating the integration of related females and unrelated males. Given that free-ranging collared peccaries can switch groups (Miller et al., 2017; Schweinsburg, 1971) and the successful introduction of unrelated individuals into captive groups has been documented (Nogueira et al., 2004; Nogueira-Filho et al., 1999), we do not expect that the introduced males would be rejected. Based on the findings in non-human primates by Sapolsky (2005) and Wittig et al. (2016), we also expected that more dominant individuals would exhibit higher concentrations of glucocorticoid metabolites in their feces.

2. Material and Methods

2.1 Ethical note

The procedures employed in the present study were approved by the Ethics Committee on Animal Use at the Universidade Estadual de Santa Cruz (CEUA/UESC) under protocol number 037/21. Additionally, this work adhered to all relevant Brazilian legislation regarding the handling of wild animals as well as the principles of the "Guide for the Care and Use of Laboratory Animals: Eighth Edition" (National Research Council, 2011).

2.2 Study site and experimental animals

The study was conducted at the Laboratory of Applied Ethology, Universidade Estadual de Santa Cruz (UESC), Ilhéus, Bahia, Brazil (UTM 480 509, 8378880). Three groups of collared peccaries were housed in enclosures with an area of 360 m². The enclosures were surrounded by wire fence, 1.5 m in height, supported by eucalyptus

posts, and had earthen floors with vegetation consisting of spaced trees that allowed complete visibility. Each enclosure contained a water trough (0.6m long × 0.4m wide × 0.3m high) and two feeders (1.0m in diameter × 0.2m wide × 0.3m high) made from recycled tires. The animals were fed twice a day, at 10:30 am and 5:30 pm, at a rate of 3.5% of their body mass, with a diet composed of a mixture of corn, soybean meal, and mineral salts, providing 12% crude protein and 3300 kcal/kg gross energy, to meet the needs of adult peccaries (Borges et al., 2017); water was available *ad libitum*.

We observed three groups of collared peccaries, each consisting of six individuals (two males and four females) (Table 1), all born and raised in captivity. Each animal was identified with plastic ear tags, cut into different shapes for identification from a distance. The groups were formed two months before the start of data collection, with the males in each group sourced separately from the females to avoid the deleterious effects of inbreeding (Nogueira-Filho et al., 1999). Initially, all the females were housed together in a single group at the Laboratory of Applied Ethology at UESC. Similarly, the males, acquired from a commercial breeder, were also housed together in a single group. During the formation of the study groups, four randomly selected females were introduced into each of the previously described experimental enclosures, which had already been populated with two adult males from the commercial breeder. We weighed the animals at the time of capture to form the groups.

Table 1. Sex (F: female; M: male) and initial body weight of the collared peccaries used across the studied groups.

G1			G2			G3		
ID	Sex	Body weight (kg)	ID	Sex	Body weight (kg)	ID	Sex	Body weight (kg)
1F	F	26.1	1F	F	24.1	1M	M	21.0
2F	F	22.6	2F	F	26.0	2F	F	17.2
3F	F	25.1	3M	M	24.9	3M	M	15.7
4M	M	23.6	4F	F	23.0	4F	F	22.1
5M	M	25.6	5F	F	23.2	5F	F	20.1
6F	F	22.7	6M	M	21.6	6F	F	14.5

2.3 Data collection

For 30 days before the data collection period, the animals were habituated to the presence of the observer, who remained in front of each enclosure, 2.0 m apart from the wire fence. Data collection involved continuous recording of social interactions in which each individual participated, either as an author or recipient (Table 2), over a 5-minute period. We considered a social interaction to occur when a collared peccary approached another to within 1.0 m, followed by a response from the approached animal, which could be either agonistic or affiliative, following Byers and Bekoff (1981). Observations were conducted over 60 non-consecutive days, with two daily sessions—one before feeding and one during feeding—each lasting 1 hour. This resulted in a total of 400 minutes of observation per individual and 120 hours of total data collection. Groups were randomly selected for observation before the start of each session, and all animals were visible during data collection. Observations concluded when at least three interactions were recorded for each dyad in the groups according to de Vries (1998).

156 Table 2. Description of the agonistic and affiliative behavioral patterns selected for
157 analysis

Category	Behavioral pattern	Description*
Agonistic	Erecting the hair	The animal erects the hairs of the mane region and, occasionally, the area of the scent gland.
	To recline	An animal assumes an arched posture with its head lowered, ears flattened, hindquarters raised, and forelegs tucked under its body. Typically, it first reclines by kneeling on its front legs before possibly lowering its hind legs.
	Teeth clacking	An animal performs rapid jaw movements, producing a series of clacking sounds.
	Lowering the head	An animal lowers its head in front of another.
	Altercation	Two individuals raise their snouts and move them laterally, emitting grunts or growls and typically making teeth-clacking movements.
Affiliative	Social grooming	An animal touches different regions of another individual's body with its nasal disk, which may be followed by licking movements and gentle biting.
	Contact sniffing	An animal extends its neck forward and gently touches its nasal disk to parts of another individual's body, initiating upward movements.
	Lying together	An animal approaches another lying individual, reclined, and lies down, touching the recipient.
	Mutual rubbing	After approaching another, an animal moves to position itself side by side but in a head-to-tail orientation with their sides touching, and they

	simultaneously rub the sides of their heads up and down against the dorsal gland area.

158 * Descriptions adapted from the study by Byers and Bekoff (1981) and Silva et al.,
159 (2020)

160 **2.4 Concentration of fecal glucocorticoid metabolites (fGM)**

161 The use of fecal glucocorticoid metabolite (fGM) assays was validated as a non-
162 invasive method for monitoring stress in collared peccaries by Coradello et al. (2012).
163 Fecal sampling was conducted opportunistically using the following procedures. During
164 observation sessions, the animals and the locations where they defecated were
165 identified. At least three fecal samples were collected from each individual. These
166 samples were collected immediately after each observation session and stored in labeled
167 plastic containers and refrigerated at -20°C for later analysis, following the
168 methodology described by Coradello et al. (2012), which is briefly summarized below.
169 After data collection, the samples were homogenized, and a sub-sample of 1-2g of feces
170 from each sample was taken, re-stored at -20°C, and then subjected to lyophilization
171 (FreeZone® Plus 4.5 Liter Cascade Benchtop, LABCONCO). Following, each sample
172 was manually ground and placed in 2.0mL plastic tubes to determine the concentration
173 (ng^{-1}) of fecal glucocorticoid metabolites in these samples, using the method described
174 by Coradello et al. (2012), at the Laboratory of Behavioral Physiology, Federal
175 University of Rio Grande do Norte, Natal, Brazil. In this laboratory, 0.1g of the fecal
176 sample was extracted with 1.0 mL of 80% ethanol, at a ratio of 0.1g - 1mL of ethanol
177 (1:10) (Coradello et al., 2012).

178 The concentrations of glucocorticoid metabolites in fecal samples (fGM) were
179 determined using an enzyme-linked immunosorbent assay (ELISA), employing a
180 polyclonal antibody for cortisol (R4866; dilution 1:8500) and a cortisol-HRP conjugate
181 (1:20000) provided by Coralie Munro (University of California, Davis, CA, 95616,
182 USA). The cross-reactivity for the antibody was 100% with cortisol, 9.9% with
183 prednisolone, 6.3% with prednisone, and 5% with cortisone. The intra- and inter-assay
184 coefficients of variation (CV) were 2.7% and 7.1%, respectively, and the assay
185 sensitivity was 7.2 ng g^{-1}.

186 **2.5 Analysis of social structure and social network**

187 To describe the social structure of the collared peccary groups, two linearity indices
188 were determined, namely the corrected Landau's linearity index (h'), adjusted for

unknown relationships (De Vries, 1998) and the triangular transitivity index (t_{tri}) (Shizuka and McDonald, 2012). Both methods evaluate the tendency of triads to be linear (e.g., A dominates B and C, B dominates C) rather than circular (e.g., A dominates B, B dominates C, and C dominates A). However, while the h' index describes the transitivity of dominance relationships in the context of tournaments, the t_{tri} index quantifies the proportion of transitive triads among all triads where all dominance relationships have been established and thus could be transitive (Shizuka and Mcdonald, 2012). Both indices range from 0.0 (non-linear hierarchy) to 1.0 (perfectly linear hierarchy). The statistical significance of h' and t_{tri} was provided through a re-sampling procedure using 10,000 randomizations (Schmid and de Vries, 2013; Shizuka and McDonald, 2012). For these analyses, the EloRating package from R software was used (Neumann and Fischer, 2023). Subsequently, we determined the directional consistency index (DCI) (Hoof, et al., 1987). The DCI assesses the direction of dominance within the hierarchy, with values ranging from 0.0 (equal exchange of dominance acts) to 1.0 (complete unidirectionality), indicating a highly structured and stable social hierarchy (Hoof et al., 1987).

Subsequently we obtained social network analysis (SNA) indices from two matrices, one containing agonistic interactions and the other affiliative interactions. In these matrices, the cell entries indicate the frequency of observed interactions for each dyad. In a social network, individuals are considered nodes or edges, and the connections between individuals are the links (Farine and Whitehead, 2015; Rose and Croft, 2015). For each network (agonistic and affiliative interactions) of each group, we calculated the eigenvector centrality indices. In directed networks, eigenvector centrality considers the direction of connections, distinguishing between those that flow toward the node (in-degree) and those that flow from the node (out-degree). A node is considered central not only if it has many direct connections but also if it is connected to other influential nodes (Sosa et al., 2021). General network measures such as density and assortativity were also calculated for each network of each group. Network density measures the ratio of the actual number of connections (edges) within a network to the maximum possible number of connections. The density values in a social network range from 0 (completely disconnected) to 1.0 (fully connected). In agonistic networks, high density can imply increase competition due to frequent interactions, while low density might suggest more dispersed or hierarchical social structures (Farine and Whitehead, 2015)

Assortativity in a social network quantifies the tendency of individuals to associate with others based on a particular attribute, such as sex. Positive values close to 1.0 indicate homophily, where individuals preferentially associate with others of the same sex. Conversely, negative values close to -1.0 indicate heterophily, where individuals more readily interact with those of the opposite sex (Sosa et al., 2021). For social network analyses, the Igraph package of the R software was used (Csardi and Nepusz, 2006).

2.6 Dominance ranking

A matrix of dominance interactions between dyads was created for each group. Individuals were ranked using the modified David's Score (MDS), and the I&SI method was then employed to determine the most consistent ranking order, following De Vries (1998) and Schmid and De Vries (2013). The dominance ranking among individuals in each group was also evaluated using Elo-rating (ER) and randomized Elo-rating (RER) (Neumann and Fischer, 2023). RER is based on the sequence in which agonistic interactions between dyads occur within a group (Neumann et al., 2011). At the start of ranking, each individual receives an initial score. The winner of an agonistic interaction gains points while the loser loses points (Elo, 1978). An initial score of 1000 points and a constant *k* of 200 were set, following Neumann (2011).

After evaluating the Elo-rating, the randomized Elo-rating was obtained by randomizing the order of interactions among individuals (1000 randomizations). Each randomization generated different individual rankings, from which average scores for each individual were calculated. We also used randomizations to estimate a 95% confidence interval for the rankings, providing an estimate of the uncertainty associated with each individual's ranking (Neumann and Fischer, 2023).

The hierarchy steepness index was calculated for each group to quantify disparities in dominance rankings, complementing the linearity index in describing social structure. This index measures the degree of difference in the ability to win agonistic interactions between individuals of adjacent rank within a social hierarchy (de Vries et al., 2006). A high steepness value, near or equal to 1.0, indicates substantial differences in conflict-winning abilities.

To determine the steepness, we used the methods proposed by de Vries et al. (2006) and Neumann and Fischer (2023). De Vries et al.'s (2006) method uses normalized scores derived from the modified David's score, whereas Neumann and Fischer's (2022) approach employs the expected probability of victory based on

individual scores obtained from randomized Elo rankings. The slope is then modeled within a Bayesian framework, yielding posterior distributions instead of point estimates of steepness. For these analyses, we used the EloSteepness package from the R software (Neumann and Fischer, 2023).

3. Analyses and Statistics

We compared differences in body weight and fecal glucocorticoid metabolite (fGM) concentrations using a general linear model (GLM) for each variable (body weight and fGM). Tukey's post-hoc tests were conducted where applicable. In these models, the group (G1, G2, and G3) and the sex (male and female) were considered as fixed factors, along with their interactions. The residuals of these models were visually inspected for normality and homoscedasticity and were deemed satisfactory. Following that, we analyzed the occurrences of agonistic and affiliative interactions between dyads of collared peccaries using a generalized linear mixed model (GLMM) for each type of interaction (agonistic or affiliative), followed by Tukey's post-hoc tests when appropriate. In these models, the group (G1, G2, and G3), the sender's sex, and the receiver's sex (male or female) were considered as fixed factors, along with their interactions. The identities of the sender and receiver, nested within their groups, were included as random factors. The residuals of these models were also visually inspected for normality and homoscedasticity and were considered adequate.

We also compared the eigenvector centrality values in agonistic and affiliative networks using GLMM, followed by Tukey's post-hoc tests when appropriate. In this model, the type of interaction (agonistic and affiliative), the group (G1, G2, and G3), and the sex (male or female) were considered as fixed factors, along with their interactions. The identities of the individuals nested within their groups were included as random factors. The residuals of these models were also visually inspected for normality and homoscedasticity and were considered adequate.

Spearman's correlation tests were conducted to assess the agreement between ranking methods (MDS, I&SI, ER, and RER). The I&SI values follow an ordinal ranking scale, where the most dominant individuals receive lower values (1, 2, 3 etc.). Thus, to avoid potential inversions in correlations between I&SI and other ranking methods, I&SI values were multiplied by -1. Spearman's correlation tests were also used to examine the relationship between dominance ranking, the position of individuals in affiliative and agonistic interaction networks, and to investigate the

relationship between ranking, weight, and fecal glucocorticoid metabolite concentrations. For all analyses, the significance level was set at $\alpha \leq 0.05$.

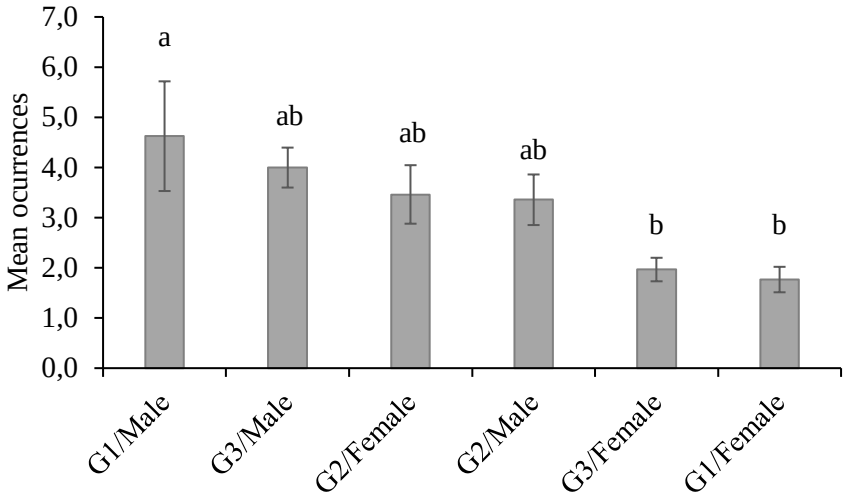
4. Results

4.1 Body weight and concentration of fecal glucocorticoid metabolites (fGM) across sexes and groups

There were no significant differences between males and females in terms of initial body weight ($F_{1, 12} = 1.40$. $p = 0.260$, males: mean = 21.3, standard error (*se*) = 1.55, females: mean = 22.6, *se* = 0.94) or fecal glucocorticoid metabolite concentrations ($F_{1, 12} = 1.14$, $p = 0.308$. Males: mean = 31.0 ng g^{-1}, *se* = 2.62. Females: mean = 32.7 ng g^{-1}, *se* = 2.63) (see SM1 for the glucocorticoid metabolite concentrations of each individual). However, the mean body weight varied between the groups ($F_{2, 12} = 11.54$, $p = 0.002$). *Post hoc* tests showed that the animals in G3 had a lower mean body weight compared to the other two groups (G1: mean body weight = 24.3 kg, *se* =0,61 and G2: mean body weight = 23.8 kg, *se* = 0.63 G3: mean body weight = 18.4 kg, *se* = 1.26). No differences were observed between the groups regarding fecal glucocorticoid metabolite concentrations in the collared peccaries (G1: mean = 26.9 ng g^{-1}, *se* = 3.23; G2: mean = 34.9 ng g^{-1}, *se* = 3.37; G3: mean = 34.6 ng g^{-1}, *se* = 2.73; $F_{2, 12} = 2.43$, $p = 0.130$). Moreover, there was no significant interaction effect between group and sex on either body weight ($F_{2, 12} = 0.26$, $p = 0.773$) or fecal glucocorticoid metabolite concentrations ($F_{2, 12} = 0.26$, $p = 0.775$).

4.1 Social structure

Throughout our observations, we recorded a total of 69 agonistic interactions among collared peccaries. There was no significant difference in these interactions between their groups (G1: total count = 23; mean per dyad = 2.6, standard error (*se*) = 0.5; G2: total count = 21; mean per dyad = 3.4, *se* = 0.4; G3: total count = 25; mean per dyad = 2.4, *se* = 0.2; $F_{2, 17.5} = 0.16$, $p = 0.858$). There were significant effects of the interactions between group and receiver's sex ($F_{2, 50.3} = 3.56$, $p = 0.036$) and between sender's sex and receiver's sex ($F_{1, 51.3} = 8.27$, $p = 0.006$). *Post hoc* tests revealed that males in G1 received more agonistic interactions than the females in the same group and those in G3 (Figure 1 a). Additionally, males directed more agonistic interactions towards other males compared to females within their groups (Figure 1 b).



b)

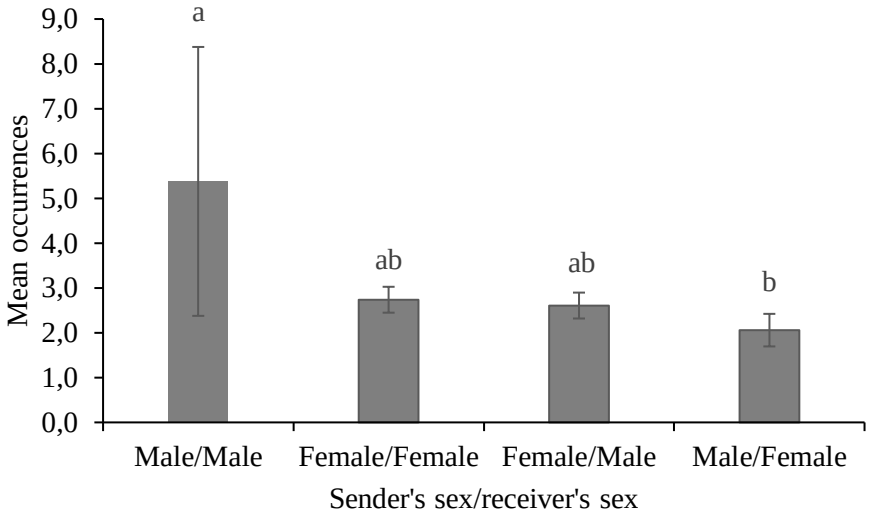


Figure 1. Mean occurrences per dyad of agonistic interactions among individuals in three captive groups of collared peccaries, categorized by the interaction between group and receiver's sex (a), and between sender's sex and receiver's sex (b).

From the agonistic interactions, we determined that the hierarchical linearity indices (h' and ttri) were close to or equal to 1.0 only in G1. However, despite being significant, the steepness in G1 based on the modified David's score was 0.41 (Table 3). Furthermore, the mean values for DCI and steepness based on the modified David's

score across the three groups were nearer to 0.0 than to 1.0 (mean DCI =0.49, se = 0.06; mean steepness = 0.34, se = 0.03).

Table 3. Total number of agonistic interactions, mean frequency (standard error) of agonistic interactions per dyad (mean frequency), and hierarchical metrics (*h*', t_{tri}, DCI, and steepness) * across three captive groups of collared peccaries.

Group	Agonistic interactions	Mean frequency	*h'*	*p*	*ttri*	*p*	DCI	steepness	*p*	Elo steepness	SE
G1	58	3.9 (0.5)	0.82	0.05	1.00	0.01	0.58	0.41	0.01	0.60	0.08
G2	60	3.0 (1.4)	0.77	0.12	0.93	0.18	0.37	0.30	0.49	0.42	0.09
G3	59	3.9 (1.1)	0.62	0.21	0.87	0.24	0.52	0.32	0.16	0.39	0.06

*Hierarchical metrics – h': the corrected Landau's linearity index adjusted for unknown relationships (de Vries, 1998); *ttri*: the triangular transitivity index; DCI: directional consistency index; steepness: steepness based on the modified David's score; and Elo steepness: mean steepness based on the randomized Elo-rating.

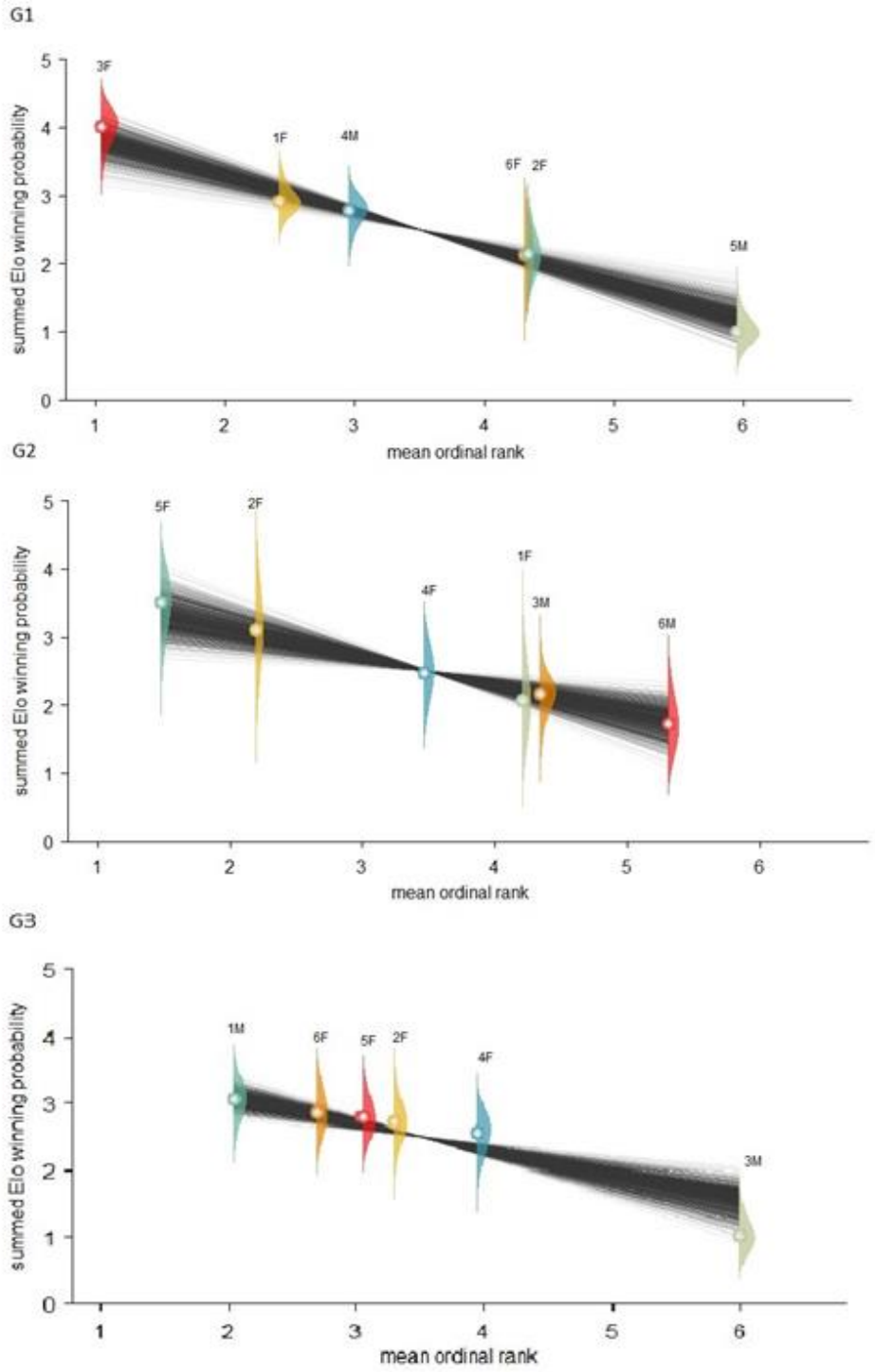


Figure 2. Elo steepness of the three captive groups of collared peccaries. The width of the posterior distribution for each individual represents the level of uncertainty in the ranking estimates. Individuals are identified by numbers (1 to 6), followed by letters denoting their sex (M: male; F: female).

During observations, we recorded a total of 63 affiliative interactions among collared peccaries, equating to 0.5 affiliative interactions per hour of observation. There

was no significant difference in these interactions between their groups (G1: total count = 21; mean per dyad = 3.1, *se* = 0.5; G2: total count = 22; mean per dyad = 3.4, *se* = 0.4; G3: total count = 22; mean per dyad = 2.5, *se* = 0.4; $F_{2, 20.6} = 0.70$, $p = 0.507$). The occurrence of affiliative interactions was not affected by the sender's sex ($F_{1, 32} = 1.56$, $p = 0.221$) nor the receiver's sex ($F_{1, 50.1} = 0.93$, $p = 0.338$). There were also no significant effects of the interactions between group and sender's sex ($F_{2, 15.1} = 0.21$, $p = 0.815$) group and receiver's sex ($F_{2, 46.7} = 2.99$, $p = 0.060$) and between sender's sex and receiver's sex ($F_{1, 50} = 1.28$, $p = 0.263$).

4.2. Social network analysis

Both the agonistic and affiliative network density indices showed relatively high values across all groups, ranging from 0.66 to 0.83 (Table 4). This indicates heightened competition as well as affiliative interaction resulting from frequent encounters. The eigenvector centrality values of the affiliative interactions were higher than the agonistic ones (affiliative: eigenvector centrality mean = 0.81, *se* = 0.05; eigenvector centrality agonistic: mean = 0.63, *se* = 0.07; $F_{1, 12} = 5.51$, $p = 0.037$). Additionally, the interaction between sex and type of interaction had a significant effect on the eigenvector centrality values ($F_{1, 12} = 11.01$, $p = 0.006$) (Supplementary material 1 provides the full model outcomes). *Post hoc* tests revealed that males in affiliative networks exhibited higher eigenvector centrality than in agonistic interactions (males in affiliative interactions: eigenvector centrality mean = 0.94, *se* = 0.04; males in agonistic interactions: eigenvector centrality mean = 0.50, *se* = 0.16). In contrast, the females' eigenvector centrality values did not differ according to the type of interaction (females in affiliative interactions: eigenvector centrality mean = 0.77, *se* = 0.06; females in agonistic interactions: eigenvector centrality mean = 0.05, *se* = 0.16). On the other hand the eigenvector values were not affected by the group ($F_{2, 12} = 0.54$, $p = 0.596$) (see Supplementary material 1 for more information).

The assortativity indices for both agonistic and affiliative interactions exhibited negative values (Table 4), indicating a preference for interactions with individuals of the opposite sex. These patterns were most pronounced in the agonistic network of G3 and least evident in the affiliative network of G1 (Figure 3).

Table 4. General network measures showing density and assortativity for affiliative (AF) and agonistic (AG) networks of three groups of collared peccaries.

Social Network Indexes			
Group	Network	Density	Assortativity
G1	AF	0.70	-0.05
	AG	0.76	-0.14
G2	AF	0.66	-0.25
	AG	0.80	-0.17
G3	AF	0.73	-0.26
	AG	0.83	-0.29

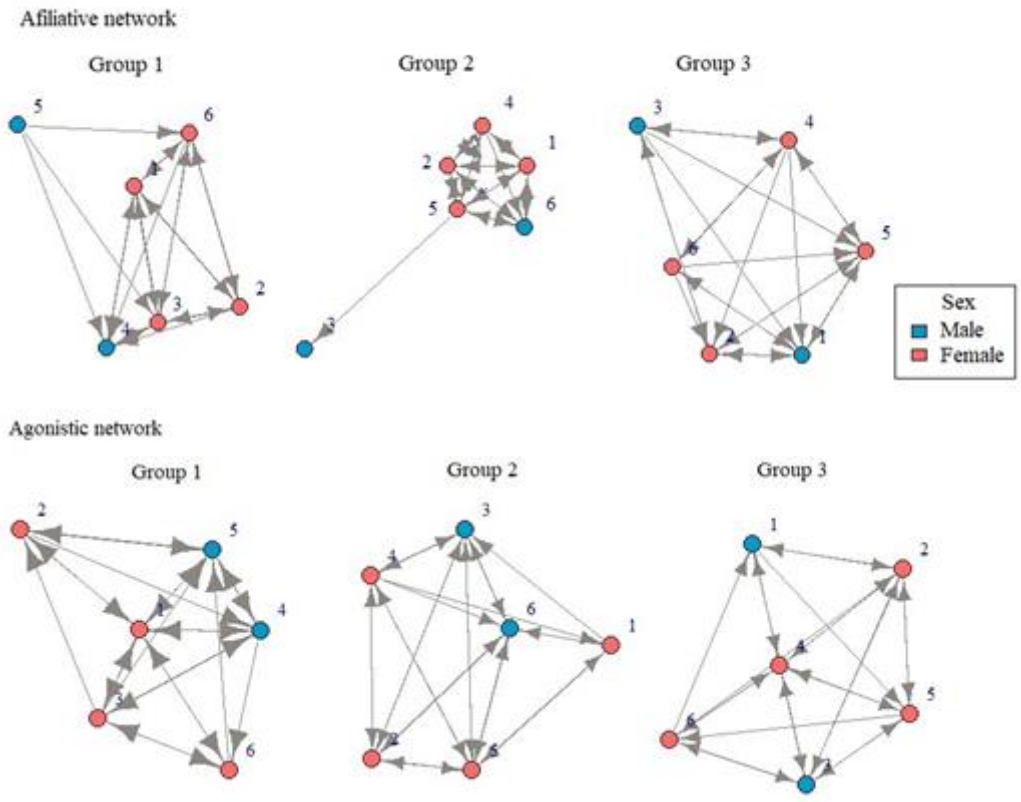


Figure 3 - Directed networks of agonistic and affiliative interactions in three captive groups of collared peccaries. The length of the arrows indicates the frequency of interactions between individuals (shorter arrows represent more frequent interactions).

4.4 Correlation among methods used to assess dominance ranking scores

There were positive correlations between the dominance rankings obtained by the ERR and MDS methods in groups G1 and G3 (Table 5). The ranking obtained by the I&IS method showed positive correlations with the rankings obtained by the ERR and MDS methods in groups G1 and G2 (Table 5). Positive correlations were found between the rankings obtained by the ERR and MDS methods and body weight in group G1, and between body weight and the I&IS method in group G2 (Table 5).

In two of the three groups (G1 and G2), there was agreement among the four dominance ranking methods in identifying the most dominant individual (Table 6). In these groups, a female held the top rank in dominance. However, in G3, this consistency was not observed. Male M1 held the top rank according to both the ER and ERR methods, while female F5 was identified as the most dominant individual by the I&SI method, and F6 had the highest score according to the MDS method (Table 6). On the other hand, in all groups, one of the introduced males occupied the rank of the most submissive individual according to all but the Elo-rating (ER) method (Table 6). On the other hand, the greatest inconsistency is observed in the intermediate rankings. The identity of the individuals occupying ranks 2 to 5 varies from method to method (Table 6), indicating that the hierarchy had not yet stabilized when we made the observations.

Table 6. Dominance ranking scores across three captive groups of collared peccaries (G1, G2, G3), assessed using four methods: inconsistencies and strengths of inconsistencies (I&SI), modified David's score (MDS), Elo-rating (ER), and randomized Elo-rating (RER)

	G1					G2					G3			
ID	I&SI	MDS	ER	RER	ID	I&SI	MDS	ER	RER	ID	I&SI	MDS	ER	RER
1F	2	2.54	61.33	64.06	1F	4	1.58	*-204.54*	3.65	1M	4	2.95	**256.84**	**62.37**
2F	3	-0.96	*-307.76*	-48.27	2F	2	0.97	-268	44.73	2F	3	0.20	212.46	34.09
3F	**1**	**7.31**	**305.97**	**211.39**	3M	*6*	*-6.02*	-176.76	*-82.63*	3M	*6*	*-7.86*	6.30	*-193.41*
4M	4	-0.08	48.22	15.07	4F	3	2.50	137.2	15.75	4F	5	-1.18	-54.23	-12.08
5M	*6*	*-7.31*	85.32	*-205.53*	5F	**1**	**4.21**	**386.96**	**120.34**	5F	**1**	2.40	*-160.51*	55.01
6F	5	-1.49	-193.10	-36.73	6M	5	-3.25	125.14	*-101.85*	6F	2	**3.50**	-206.87	54.01

* The top-ranked individuals in each group are highlighted in bold, while the most submissive ones are indicated in italics, according to the ranking assessment methods.

4.4.1 Correlations between dominance ranking scores, concentration of fecal glucocorticoid metabolites (fGM), eigenvector centralities, and body weight

Fecal glucocorticoid metabolite (fGM) concentrations were positively correlated with the dominance ranking obtained by the MDS method in group G2 and with the ranking obtained by the I&SI method in group G3 (Table 5). There was also a positive correlation between the ranking obtained by the ERR method and the eigenvector centrality of agonistic interactions (EC_AG) across all three groups (Table 5). Positive correlations were further observed between the ranking obtained by the MDS method and EC_AG in group G1, and between EC_AG and body weight in groups G1 and G2 (Table 5). Additionally, there was a negative correlation between the ranking obtained by the MDS method and the eigenvector centrality of affiliative interactions (EC_AF) in group G3 (Table 5).

Table 5. Spearman correlation coefficients ($r_{Spearman)}$ between the dominance ranking scores across three groups (G1, G2, G3) of captive collared peccaries assessed using the following methods: inconsistencies and strength of inconsistencies (I&SI), modified David's score (MDS), elo-rating (ER), and randomized elo-rating (RER), and between these scores and individuals' body weight (BW), eigenvector centrality of agonistic interactions (EC_AG) and affiliative interactions (EC_AF), and fecal glucocorticoid metabolite concentrations (fGM) in the three groups of collared peccaries.

		G1		G2		G3	
Variable 1	Variable 2	$r_{Spearman}$	*p*	$r_{Spearman}$	*p*	$r_{Spearman}$	*p*
ERR	ER	0.43	0.396	0.20	0.704	0.09	0.871
ERR	**MDS**	**0.94**	**0.004**	0.77	0.072	**0.83**	**0.041**
ER	MDS	0.37	0.468	0.54	0.265	-0.26	0.622
ERR	**I&IS**	**0.83**	**0.041**	**0.94**	**0.004**	0.66	0.156
ER	I&IS	0.26	0.622	0.26	0.622	-0.49	0.328
MDS	**I&IS**	**0.94**	**0.004**	**0.83**	**0.041**	0.71	0.11
ERR	**BW**	0.77	0.072	**0.83**	**0.041**	0.37	0.468
ER	BW	0.49	0.328	0.37	0.468	-0.26	0.622
MDS	**BW**	**0.89**	**0.018**	0.71	0.11	0.20	0.704
I&IS	**BW**	0.77	0.072	**0.94**	**0.004**	0.26	0.622

ERR	fGM	-0.03	0.957	0.43	0.396	0.41	0.424
ER	fGM	0.37	0.468	0.66	0.156	-0.26	0.617
MDS	**fGM**	-0.14	0.787	**0.89**	**0.018**	0.38	0.461
I&IS	**fGM**	-0.09	0.871	0.54	0.265	0.84	**0.036**
BW	fGM	-0.37	0.468	0.49	0.328	-0.17	0.741
ERR	**EC_AG**	**0.94**	**0.004**	**0.89**	**0.018**	**0.83**	**0.041**
ER	EC_AG	0.37	0.468	0.09	0.871	0.49	0.328
MDS	**EC_AG**	**0.89**	**0.018**	0.77	0.072	0.60	0.208
I&IS	**EC_AG**	0.71	0.11	**0.94**	**0.004**	0.49	0.328
BW	**EC_AG**	**0.83**	**0.041**	**0.83**	**0.041**	0.14	0.787
fGM	EC_AG	-0.31	0.544	0.43	0.396	0.41	0.424
ERR	EC_AF	-0.09	0.871	-0.37	0.468	-0.66	0.156
ER	EC_AF	0.60	0.208	0.20	0.704	0.03	0.957
MDS	**EC_AF**	-0.14	0.787	-0.60	0.208	**-0.89**	**0.018**
I&IS	EC_AF	-0.37	0.468	-0.43	0.396	-0.54	0.265
BW	EC_AF	0.14	0.787	-0.20	0.704	0.26	0.622
fGM	EC_AF	0.26	0.622	-0.60	0.208	-0.41	0.424
EC_AG	EC_AF	-0.03	0.957	-0.49	0.328	-0.60	0.208

*Bold values indicate significant correlation ($p < 0.05$).

5. Discussion

Our findings revealed the absence of a clear dominance hierarchy among captive collared peccaries. It was only in G1 that both Landau's linearity index (h') (de Vries, 1998) and the triangular transitivity index (ttri) (Shizuka and McDonald, 2012) indicated a linear dominance structure. However, in G2 and G3, both h' and ttri showed near-linear values, but their probabilities of being distinct by chance were lower. This supports Appleby's (1983) observation that smaller group sizes inherently increase the likelihood of linear hierarchies arising by chance. Additionally, the mean indices for the DCI (Hoof et al., 1987) and steepness (de Vries et al., 2006; Neumann and Fischer, 2023) were closer to 0.0, indicating inconsistent asymmetries between individuals and a lack of predictability in agonistic interactions. Therefore, our results corroborate Nogueira-Filho et al.'s (1999) suggestion that egalitarian rather than hierarchical relationships characterize the social structure of collared peccaries. This finding also supports the observation made by Byers and Bekoff (1981), who found no evidence of dominance hierarchies among free-ranging collared peccaries.

On the other hand, Dubost (2001) found that captive collared peccaries were organized into two separate linear dominance hierarchies for males and females. In contrast, Bissonette (1982) reported a single linear dominance hierarchy in free-ranging peccary herds, with males always being dominant. However, both studies assumed a linear dominance hierarchy without calculating linearity indices or using statistical tests. In a study by Silva et al. (2016), the Elo-rating method was used to study dominance relations in four groups of captive collared peccaries. They found that two groups exhibited a linear dominance hierarchy, including both males and females, while the other two groups had a linear dominance hierarchy with females in the highest-ranking positions. Thus, the lack of a linear dominance hierarchy characterizing the social structure of collared peccaries could be explained by the fact that the hierarchy had not yet been established, which we expected to occur during the 30-day habituation period. This expectation is justified because, typically, dominance rankings are established during initial encounters between animals through repeated threats and fights. Once these rankings are defined, each individual displays minimal hostility towards its superiors, resulting in the exhibition of ritualized signals between dominants and subordinates (Eibl-Eibesfeldt, 1970; Wilson, 1975). Thus, even with the complementary methods adopted here to characterize the social structure of collared peccaries, the existence of a linear hierarchy in collared peccary groups remains controversial (Biondo, 2014).

Although no clear hierarchy was observed among the collared peccaries, the dominant and submissive behavioral patterns exhibited by the animals effectively prevented the escalation of violence, as no bites or injuries were recorded. The frequency of agonistic interactions did not significantly differ across groups but showed distinct sex-based patterns. Males in G1 received significantly more agonistic interactions than females in the same group or males in G3. Notably, males were introduced to groups with already established female members, potentially intensifying agonistic interactions among males. This was evident from the higher frequency of male-directed agonistic interactions, even at 30 days post-introduction, when observations began. These patterns are consistent with findings in other social species, where male-male interactions often reflect competition for dominance or resources (Clutton-Brock and Huchard, 2013).

The most submissive individuals, typically the introduced males, displayed greater centrality in affiliative networks. This suggests they employ affiliative strategies to foster social bonds and alleviate tensions, similar to behaviors observed in non-human primates (Romero et al., 2009; Sapolsky et al., 2000). Moreover, contrary to expectations, a significant negative correlation between dominance rank and centrality in affiliative networks was observed in G3 when using MDS. This finding suggests that subordinate individuals may engage more in affiliative behaviors, possibly as a strategy to build alliances or reduce social tensions within the group. This proposition is supported by the negative values for assortativity in both agonistic and affiliative networks, indicating a preference for interactions with individuals of the opposite sex. The introduction of new males might have amplified the negative assortativity in both network types. The long-term effects of such introductions on social dynamics and behavior warrant further study, particularly after the stabilization phase.

The correlations between dominance ranking, network centrality, hormone levels, and body weight yielded mixed results. While significant correlations among these variables were found in some groups, these relationships were not consistent across all groups. Despite suggesting an apparent rank order, the classification of individuals is accompanied by uncertainty. This can also be verified by the high agonistic network density values, indicating frequent challenges among individuals without clear resolution, leading to more circular or ambiguous triadic relationships, as described by Shizuka and McDonald (2012). Consequently, the inconsistency between methods for assessing dominance rankings may reflect a less stable or more contested hierarchical structure (Balasubramaniam et al., 2013). These results reinforce the proposition that dominance relationships had not yet been established in the studied groups. Consequently, the correlations between ranking and other variables observed in the present study should be considered with caution. For instance, the hypothesis that dominant individuals occupy central positions in agonistic networks was supported across all groups using the RER method. This result aligns with theoretical expectations that high-ranking individuals are more involved in aggressive interactions, whether initiating or receiving, to establish or maintain their position. Additional support was found using MDS in G1 and I&SI in G2, suggesting that methodological differences may influence the ability to detect these correlations. The stronger consistency of the

RER method across groups suggests its robustness in assessing dominance-centrality relationships.

The hypothesis that dominant individuals exhibit higher fGM concentrations was supported in G2 (using MDS) and G3 (using I&SI), indicating that dominant individuals in these groups may experience heightened physiological stress. These findings align with studies by Sapolsky (2005) and Wittig et al. (2016), which link higher glucocorticoid levels to dominant individuals in non-human primates. This could be due to the energy and social demands of maintaining high-ranking positions. Interestingly, no relationship was found between centrality in either agonistic or affiliative networks and fGM concentrations, suggesting that centrality in social networks, irrespective of the type of interaction, may not directly correlate with stress levels.

The positive correlation between body weight and centrality in G1 and G2 suggests that larger individuals may hold more influential positions within their social networks, likely due to the advantages of greater physical size in agonistic contexts. Additionally, the link between body weight and dominance rank (using MDS in G1 and I&SI in G2) further supports the idea that body size significantly influences social hierarchy in collared peccaries, as seen in other artiodactyls like Tayassu peccary (Nogueira-Filho et al., 1999; Grossel et al., 2022) and *Sus scrofa* (Újváry et al., 2012). Two hypotheses could explain this observation: First, body weight may reflect asymmetries in fighting ability or resource-holding potential, suggesting that heavier individuals are more capable of securing food resources, thereby achieving higher dominance ranks (Parker, 1974). Second, reverse causality could be at play, where dominant individuals gain preferential access to food, leading to increased body weight (Taillon and Côté, 2007). In this case, behavioral traits such as aggressiveness and boldness enable dominant individuals to acquire resources more effectively, while submissive, less aggressive, and shyer individuals have reduced access to resources, resulting in lower body weights (Côté, 2000; Taillon and Côté, 2007).

On the other hand, the absence of a relationship between body weight and fGM concentrations implies that physical size alone does not influence physiological stress levels. However, it is important to emphasize that correlations in the present study do not imply causality, and further research is needed to clarify the relationship between stress levels and social structure, particularly in wild species kept in captivity. Future research should also explore the factors driving group-specific variations in hierarchy

and stress, as well as the implications of social network positions for individual fitness and welfare in captive populations. Moreover, despite experiencing higher levels of aggression, males did not exhibit elevated glucocorticoid metabolite (fGM) levels. The fGM concentration levels observed here were comparable to the mean baseline reported by Coradello et al. (2012), suggesting that the study conditions did not impose significant stress on both the introduced males and the resident females in these groups.

6. Conclusions

Our study highlights the intricate relationship between dominance, stress, and social network positions in collared peccaries, enhancing our understanding of their social behavior in captivity. It supports the feasibility of introducing unfamiliar males into established female groups. We found that dominance and centrality in agonistic networks are closely aligned, while affiliative interactions show subordinates in more central roles. The lack of a direct link between centrality and fGM concentrations underscores the complexity of social dynamics and stress, indicating the need to consider additional factors.

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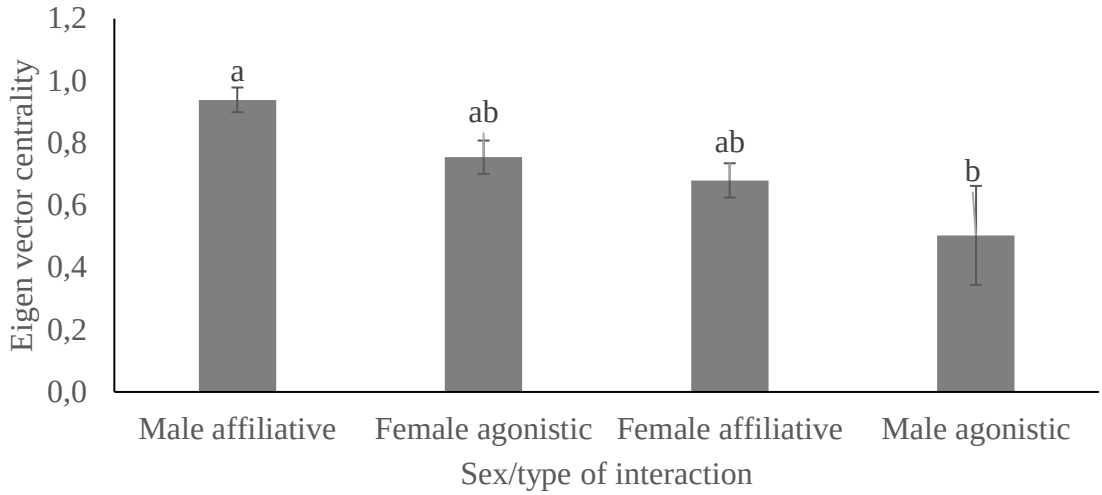
8. Supplementary material

SM 1- Results of the comparison of eigenvector centrality values between agonistic and affiliative networks using a Generalized Linear Mixed Model (GLMM). The model included the type of interaction (agonistic vs. affiliative), group (G1, G2, and G3), and sex (male or female) as fixed factors, along with their interaction terms.

Term	*Num DF*	*DenDF*	f	*p*
Group	2	12	0,54	0,596
Sex	1	12	0	0,962
Eigenvector centrality	1	12	5,51	0,037
Group*sex	2	12	0,96	0,41
Group*eigenvector centrality	2	12	0,19	0,827
sex*eigenvector centrality	1	12	11,01	0,006
Group*sex*eigenvector centrality	2	12	2,26	0,147

SM 2- Pairwise comparisons of eigenvector centrality values across interaction types (agonistic vs. affiliative) and sex (female [F] vs. male [M]).

	N	Mean	Grouping	
Sex				
M	12	0,721132	A	
F	24	0,717245	A	
Eigenvector centrality				
Affiliative	18	0,81	A	
Agonistic	18	0,63	B	
Sex*Eigenvector centrality				
M Affiliative	6	0,94	A	
F Agonistic	12	0,75	A	B
F Affiliative	12	0,68	A	B
M Agonistic	6	0,50		B



SM Figure 2- Mean eigenvector centrality values for agonistic and affiliative networks, stratified by sex (males and females).