



# Investigating the genetic and environmental architecture of interpack aggression in North American grey wolves

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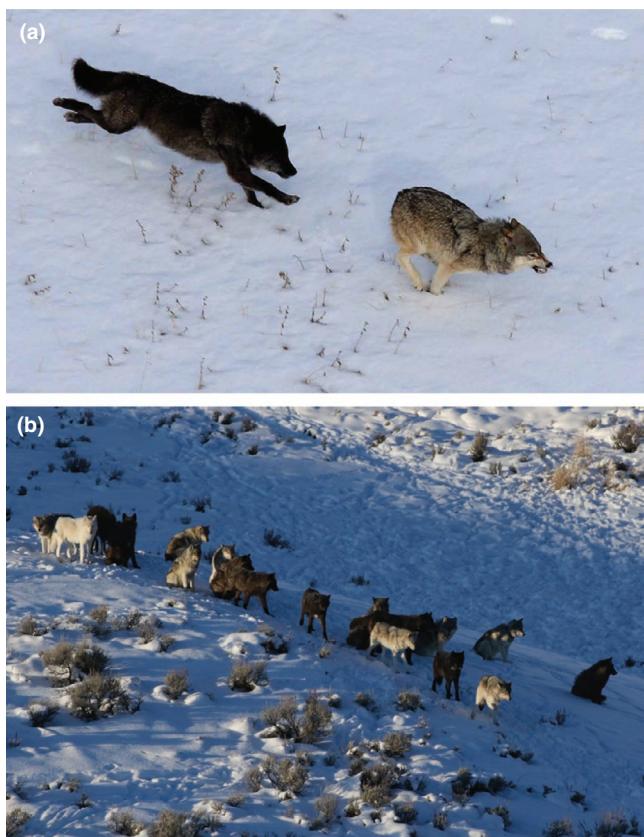
Aggression confers several fitness benefits including increased breeding opportunities and resource acquisition. Determining the relative contributions of genetic and environmental components to shaping aggression is essential for advancing our understanding of how selection affects the distribution of aggressive phenotypes in a population. In a *From the Cover* article in this issue of *Molecular Ecology*, vonHoldt et al. (2020) used RAD-seq methods to obtain genome-wide single nucleotide polymorphism (SNP) data to estimate heritability of interpack aggression of 141 North American grey wolves (*Canis lupus*) surveyed from 1995–2018. The authors inferred heritability using both a SNP-based genetic relationship matrix (GRM) and a consensus pedigree informed by: (a) previously obtained microsatellite data; (b) past observations of parentage; and (c) statistical reconstruction of parent-offspring pairs. SNP-based (i.e., GRM) and pedigree-based (i.e., consensus pedigree) heritability estimates were 37% and 14%, respectively, with an additional 14%–16% explained by natal pack effects. The study confirmed the previously discovered strong effects of relative pack size and breeding status on interpack aggression, illustrating how social dynamics and density-dependent factors induce variance in aggressive behaviours. Finally, the authors found associations between average individual aggression scores (IAS) and specific candidate genes (MYO9A and TRAK1). In sum, vonHoldt et al. (2020) provides an unprecedented and nuanced synthesis that not only suggests gene-aggression associations, but also emphasizes how additive genetic variance and density-dependent factors interact to maintain phenotypic variance in aggression over time.

## KEY WORDS

aggression, density-dependent, grey wolves, heritability, RAD-seq, stabilizing selection

Using 598 genetic samples representing 468 unique wolves in Yellowstone National Park (YNP) from 1995–2018, vonHoldt et al. (2020) explored the contribution of additive genetic variance in shaping heritable variation in interpack aggression. Interpack aggression describes when an individual aggresses an intruding conspecific from an adjacent pack (Figure 1a), and successful execution of this behaviour serves to maintain territorial boundaries, facilitating continued access to quality habitat suitable for pup-rearing and prey acquisition. Fluctuations in density-dependent factors, including prey abundance, pack size, and composition, are known to induce

plasticity in both intra- and interpack aggression levels (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Cubaynes et al., 2014). However, aggression is also moderately heritable in a variety of taxa (Araya-Ajoy & Dingemanse, 2017; Duckworth & Badyaev, 2007), including in other species of Canidae (Saetre et al., 2006), with past candidate gene approaches explicating the links between aggression and specific gene regions (van Oers, De Jong, Van Noordwijk, Kempenaers, & Drent, 2005). Investigating the contribution of additive genetic effects to aggression thus provides insight into how selection maintains aggression in populations, a particularly salient



**FIGURE 1** (a) Photo observation illustrating an interpack aggressive bout. (b) Along with additive genetic variance, factors including natal pack identity, relative pack size, maternal effects, and independent environmental effects were also considered in linear mixed models. Relative pack size was a significant predictor of individual aggression scores

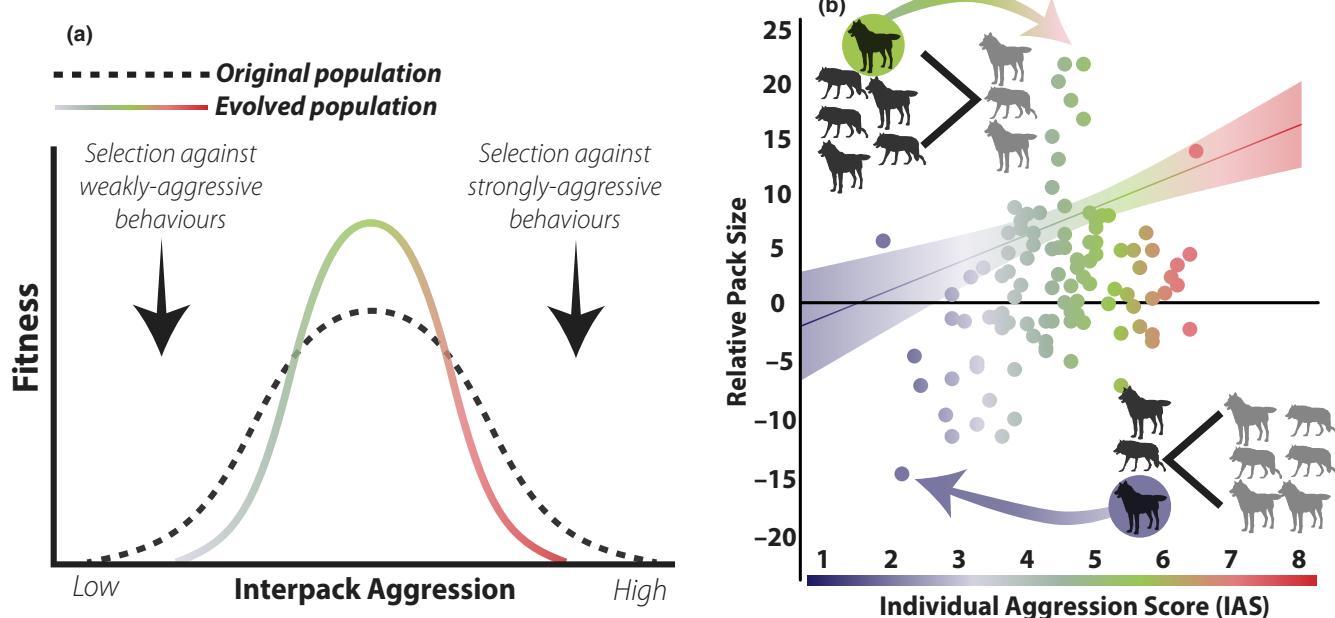
question for social species and those of conservation concern. In this study, vonHoldt et al. (2020) used parallel experimental approaches that provided converging evidence of heritability in interpack aggression and illustrated specific gene regions possibly under selection in a wild, long-lived species.

To quantify aggressive phenotypes, the authors collated multiple observations of individually recognizable wolves, ranked interpack aggression observations on an ordinal scale ranging from one (flee) to a 10 (chase led to mortality), and averaged scores within each individual to create an individual aggression score (IAS). vonHoldt et al. (2020) then constrained heritability analyses to wolves that had at least three documented interpack interactions ( $n = 141$  wolves), reducing the effect of observer or pack dynamic variance (vonHoldt et al., 2020). Using a RAD-seq protocol, they were able to retain 413 wolves with 120,327 SNPs for pedigree analysis after initial SNP filtering, duplicate SNP removal, and exclusion of missing data. Whereas the robust GRM was informed by global kinship estimates derived from 12,228 SNPs, the consensus pedigree was informed by the combination of prior microsatellite data (vonHoldt et al., 2008), and at least one of the following R packages used to calculate relatedness coefficients between parent-offspring pairs: RELATED and SEQUOIA. They then used linear mixed models (LMMs) and Akaike's

information criterion (AIC) to determine the best-fit models explaining variance in IAS, including covariates in natal pack identity, dominance, birth cohort, and residual environmental effects (Figure 1b). The best-fit model for the GRM approach included additive genetic variance, natal pack, and independent environment effects, with an SNP-based heritability estimate of  $h^2 = 0.369$ . In contrast, sole inclusion of the natal pack component best explained variance in aggression for the consensus pedigree approach, with a narrow-sense heritability estimate of  $h^2 = 0.138$ . Further, the authors observed associations between IAS and variation in several genes (MYO9A and TRAK1) that are functionally relevant for regulating GABA-A receptors, which may contribute to aggressive behaviour in animals (Golden, Jin, & Shaham, 2019). Altogether, results from vonHoldt et al. (2020) provide evidence to suggest that variation in aggression levels is both moderately heritable and modular according to intra- and interpack dynamics.

Aggression can have individual fitness benefits but can also incur substantial fitness costs that are group and context dependent. Overabundance of highly aggressive individuals within a group can lead to increased levels of both intra- and intergroup aggression that jeopardizes individual fitness. For example, overrepresentation of highly aggressive individuals in a group increases intragroup competition that drives out females, leading to overall reductions in reproduction (Sih & Watters, 2005). In contrast, groups with few or no aggressive individuals are outcompeted for resources and territory. Stabilizing selection for moderately aggressive phenotypes should thus be favored over the two extremes (Figure 2a). This study provides novel evidence to ask follow-up questions, including: (a) how group composition of aggressive phenotypes influences group and individual-level fitness; (b) whether increasing social cohesion within a pack positively impacts group performance in interpack interactions; and (c) if heritable variation in interpack aggression plays a critical role in determining pack performance. Canids maintain strict territorial boundaries that are reinforced by hierarchical dynamics within a pack, and removal of dominant individuals generally results in group collapse as neighbouring packs vie for vacated territory. In this study, the authors discuss how the loss of a specific individual in one pack led to the disintegration of three established packs (i.e., Druid Peak, Slough Creek, and Agate Creek). Specific individuals may consequently serve as social linchpins that regulate group and population-level stability, emphasizing the significance of discovering associations between certain genetic polymorphisms and behavioural phenotypes.

Relative group size and composition are also important drivers of interpack aggression (Figure 2b). vonHoldt et al. (2020) provide evidence to illustrate that IAS values are greater when relative pack size of the focal individual is greater, consistent with the earlier work of Cassidy et al. (2015). This necessarily implies that individual wolves do not aggress intruding conspecifics when the numerical odds are unfavorable, implicitly suggesting aggression is also highly contextual. However, previous work suggest that composition is equally as important as size, as packs with older individuals and more males could outcompete other packs despite numerical disadvantages



**FIGURE 2** (a) Stabilizing selection favours moderately aggressive behaviours and phenotypes, maximizing resource acquisition while minimizing potential risk of injury due to excessive conflict. (b) Relative pack size (calculated as the size of the focal individual's resident pack relative to the competing pack; negative values indicate that the focal individual's pack was smaller) positively predicted interpack aggression strength. Focal individuals from smaller packs generally exhibited smaller IAS scores relative to those in larger packs. Colour-coding schema for (a–b) and data for (b) courtesy of vonHoldt et al. (2020)

(Cassidy et al., 2015). Moreover, because wolf densities predict wolf survival (Cubaynes et al., 2014), we may hypothesize that selection for aggressive phenotypes shifts with shifting pack size and composition. Hence, the relative benefit of recruiting aggressive individuals to a pack may be dependent on the complex interplay between intra- and interpack dynamics, and selection gradients on the genes identified by the authors may fluctuate across packs over both time and context. Investigating such hypotheses are now possible with the meticulous examination of additive genetic and environmental components of aggression performed by the current study.

Determining whether behavioural variation is heritable and linked to polymorphisms in specific genomic regions is integral to informing our understanding of how selection maintains phenotypic diversity in populations (van Oers & Mueller, 2010). Results from vonHoldt et al. (2020) greatly succeed in this regard, leveraging next-generation sequencing techniques with a long-term wild pedigree population to set the foundation for future studies. In so doing, the authors not only provide a novel contribution, but also reveal several exciting future eco-evolutionary questions to investigate in grey wolves and other highly social species. This study is also incredibly rare for a large, long-lived vertebrate. The authors therefore establish an exceptional roadmap for future genomic studies interested in large or clandestine species of conservation and management concern.

#### DATA AVAILABILITY STATEMENT

Data used to create the scatterplot in this perspective were generated from data provided by vonHoldt et al. (2020) (Supporting Information). Photos of Yellowstone wolves taken by Daniel Stahler

from the National Park Service (NPS) and provided by Dr Bridgett vonHoldt.

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