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Ecological and Evolutionary Feedbacks in the Evolution of Aggression

Renée A. Duckworth

INTRODUCTION

Acts of aggression are ubiquitous among animals and play a key role in survival and reproduction. Animals often use aggressive behaviors to defend or usurp a resource (Stamps & Krishnan, 1997; Garcia & Arroyo, 2002), to compete for mates (Bartoš, 1986; Hagelin, 2002), to fend off predators (Andersson et al., 1980; Redondo & Carranza, 1989), and during foraging (Riechert, 1993). However, even though aggression is important in a number of distinct contexts, it is also a costly behavior. These costs range from direct costs in terms of energy expenditure and injury during aggressive conflicts to more subtle costs of disrupting social bonds in communally living species. A balance between costs and benefits has traditionally been the main explanation for variation in aggression observed within and among individuals as well as between populations and species; however, recent work on animal personalities has introduced the possibility that constraints may also be important to understanding this variation.

Aggression, by definition, is a social (or antisocial) behavior in that it only occurs in the context of two or more interacting individuals. At the most basic level, aggression is used to either subdue another individual (as during predation or aggressive courtship) or to repel another individual (as during

territorial defense or when fending off predators). By influencing territorial spacing, predator-prey dynamics, and social-group membership, aggressive interactions can influence how individuals arrange themselves in space and time and can have large-scale ecological consequences. The importance of evolutionary feedback effects resulting from ecological consequences of aggression is a new and exciting area of research that may prove critical to our understanding of why populations and species vary.

Partly because of the importance of aggression to fitness and partly because aggressive behaviors are relatively easy to observe and characterize in natural populations, aggression is well studied in diverse contexts and species, and thus evolutionary studies of aggression provide unique insight into the evolution of behavior more generally. In this chapter, I will first summarize recent work on personality differences in aggression to explore the novel insights this work poses for understanding the evolution of aggression, and I will then discuss the role of ecological and evolutionary feedbacks in maintaining population- and species-level differences in aggression.

WHAT IS AGGRESSIVE PERSONALITY VARIATION?

Personality variation refers to consistent differences in behavior among individuals. The study of nonhuman animal personalities is a recent addition to the field of behavioral ecology and is set against a background of several decades of research on the evolution of animal behavior from an optimality perspective (Sih et al., 2004; Bell, 2007; McNamara et al., 2009), where it is assumed that animals strategically adjust their behavior to maximize fitness given existing trade-offs (Roff, 1994). Behavioral ecologists have used this framework—which assumes that constraints to behavioral flexibility are weak or nonexistent and that behavior of individuals within a population will converge on a single optimal expression in a particular context—to predict when and how individuals should reversibly adjust their behavior in different contexts (Krebs & Davies, 1991). Yet recent studies demonstrating the ubiquity of animal personalities challenge these basic assumptions because they show that individuals are often limited in the flexibility of their behavior, that there are often pronounced differences in behavior among individuals in the same context, and that distinct behaviors are often closely correlated in expression (Dingemanse & Réale, 2005; Bergmüller & Taborsky, 2010).

A particularly puzzling component of personality variation is the remarkable consistency in behavior across contexts even when changing behavior would confer higher fitness (Sih et al., 2004). For example, in fishing spiders

(*Dolomedes triton*), females that are most aggressive in a foraging context are also most aggressive in a mating context, and aggressive females are likely to cannibalize prospective mates before copulating with them to the extent that some females attack every single male and thus fail to mate and produce off-spring (Arnqvist & Henriksson, 1997; Johnson & Sih, 2005). In another example, in many species of birds, the most aggressive males invest the least in parental care, and this often results in lower reproductive success (e.g., Tut-tle, 2003; Duckworth, 2006a; see Ketterson & Nolan, 1994, for review). These costs to inflexible expression of aggression raise the question of why individuals that behave aggressively in one context cannot modify their overall behavioral strategy to behave less aggressively in a different context.

Variation in aggressiveness has been one of the most commonly described axes of personality variation. Consistent differences in aggression have been docu-mented in insects, spiders, fish, birds, and mammals. Such stability in behavior is usually detected as significant repeatability either over time or in distinct func-tional contexts (e.g., aggression toward a rival male versus aggression towards a predator). A ***meta-analysis*** of studies that compared repeatability of 13 different classes of behavior showed that aggressive behavior was one of most highly repeat-able (Bell et al., 2009). Yet there is a rich history of work on aggression showing that it is often context dependent and strongly influenced by environmental con-ditions. For example, increases in group size and experimental decreases of food resources both independently increase the number of aggressive interactions in red deer (*Cervus elaphus*) stags (Appleby, 1980; Bartoš, 1986). Moreover, many studies of territorial animals show that individuals are more aggressive toward strangers than toward neighbors (Jaeger, 1981; Temeles, 1994), demonstrating that individuals often modulate aggressiveness depending on social context. Even abiotic conditions have been shown to influence aggressiveness—in coral reef fish (*Pomacentrus* spp.) aggressiveness increased with increases in water temperature (Biro et al., 2010). *How can we reconcile such seeming flexibility of aggression with the growing body of work that shows aggression to be highly repeatable within individ-uals?* The key to resolving this puzzle is to recognize that most studies investigating the effects of environmental variation on aggression often ignore individual varia-tion and focus instead on mean population-level changes. Moreover, high repeat-ability does not preclude the possibility that individuals modify their behavior in different situations but simply means that the rank order of aggressiveness of a group of individuals is consistent over time or across different contexts such that, even if all individuals decrease their aggressive response in a particular context, the most aggressive individuals in one context are still the most aggressive in the other (see Figure 10.1 for an example).
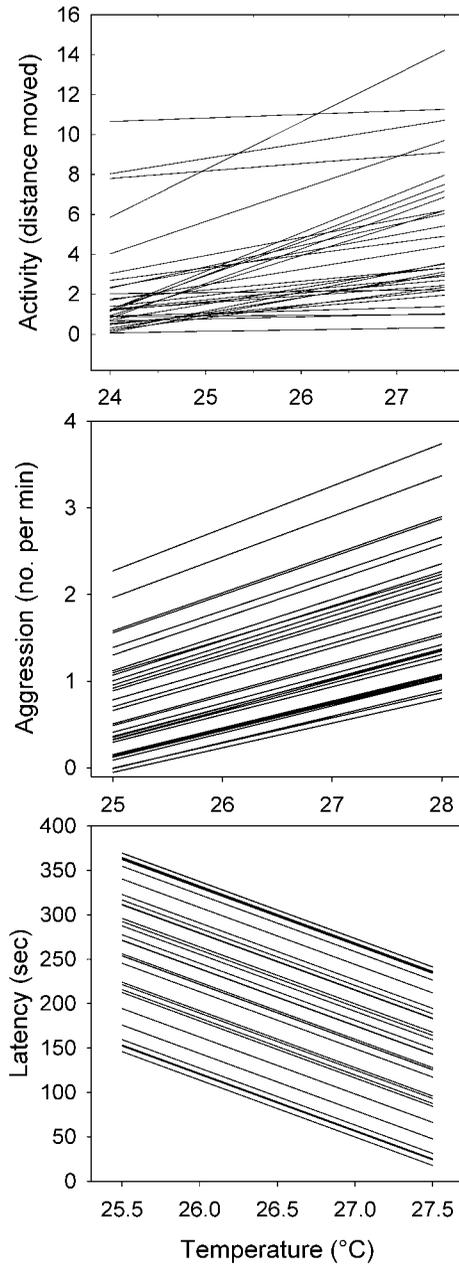
Figure 10.1. Examples of consistent individual differences in a highly plastic behavior. Coral reef fish show plasticity in activity (top graph), aggression (middle graph), and latency (bottom graph) in relation to temperature. Rank order of individuals is constant across temperatures for aggression and latency but not for activity levels. (Figure from Biro et al., 2010. Used by permission of the Royal Society.)

Such consistent differences in aggressive behavior among individuals raise several important questions. *Why do individuals show consistency in the expression of aggression even when placed in different situations where the costs and benefits of displaying aggressive behavior vary? To what extent is aggression correlated with other traits? Why do such correlations evolve, and what are their evolutionary implications? Are there any general patterns across species regarding which traits are associated with aggression? Finally, how do individual, population-, and species-level variation in aggression impact ecological and evolutionary processes?*

WHY ARE INDIVIDUALS CONSISTENT IN EXPRESSION OF AGGRESSION?

There are two main answers to these questions: ***natural selection*** favors constancy in expression (hereafter "adaptive hypothesis") or ***developmental constraints*** limit flexibility of aggression (hereafter "constraint hypothesis"). The adaptive hypothesis assumes there is unlimited potential for flexibility of aggression within individuals but that stability is adaptive. In other words, if extreme flexibility of aggression were adaptive, then it would easily evolve given enough time. Stability of aggression could be adaptive if natural selection favors either its correlation with other, less flexible traits (see below for examples) or its predictability (McElreath & Strimling, 2006; Wolf et al., 2007; McNamara et al., 2009). In contrast, under the constraint hypothesis, there are intrinsic limits to flexibility of aggression, and thus selection is assumed to play a minor or no role in the evolution of consistency (Duckworth, 2010). From this perspective, the physical structures that underlie variation in aggression, including variation in brain anatomy, neuronal connectivity, neurotransmitter synthesis and degradation, hormone secretion patterns, hormone receptor distribution, and endocrine gland function, may be limited in their flexibility, and in turn this limits flexibility of aggression. In other words, under this view, no matter the intensity of natural selection, there is a limit to how much flexibility of aggression can evolve.

The relative importance of selection and constraint in the evolution of stable differences in aggression between individuals is not clear. Many of the adaptive hypotheses predict strong correlations between aggression and other traits, and while such correlations are often found (see below for examples), it is unclear whether these correlations are a cause or consequence of limited flexibility of aggression (Duckworth, 2010). Adaptive hypotheses also predict variability among species in whether they express consistent differences in aggression, whereas the constraint hypothesis predicts that limits to flexibility should be widespread across a diversity of taxa, especially if they arise from limitations on organismal design due to physical laws (*sensu* Maynard Smith

et al., 1985; Brakefield, 2006). Evidence for high repeatability of aggression across studies supports the constraint hypothesis; however, more rigorous comparison of flexibility of aggression across a diversity of taxa as well as a comparison of developmental mechanisms underlying individuals differences in behavior are needed before any conclusions on this topic can be drawn.

Unfortunately, very little is known about the developmental basis of individual differences in aggression as most studies of behavioral development focus on larger-scale differences between the sexes, between normal and mutant phenotypes, or between species. Thus, there is currently very little data linking naturally occurring individual variation in behavior to neural and endocrine differences among individuals. However, there is some preliminary support for the idea that constraints are important. The constraint hypothesis predicts that similar developmental pathways would underlie individual variation in aggression across disparate taxa (Duckworth, 2010). Recent reviews suggest that variation in aggression is linked to variation in the serotonin signaling system (Figure 10.2) across a wide variety of species, from
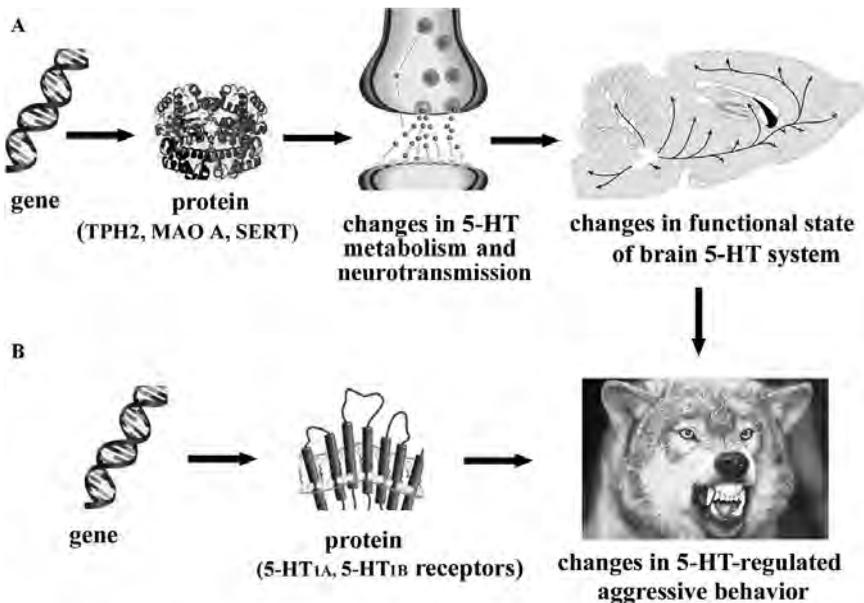

Figure 10.2.   Serotonin (5-HT) pathways that underlie variation in aggression are remarkably conserved across disparate taxa. (a) One pathway from genes to aggression involves key enzymes involved in synthesis (TPH2), degredation (MAO A), and transport (SERT) of serotonin. (b) A shorter pathway involves changes in 5-HT receptors. (Figure from Popova, 2006. Used by permission of John Wiley and Sons.)

crayfish to foxes to humans (Popova, 2006), providing some preliminary evidence for this prediction. Yet, at the same time, other physiological systems that are known to influence aggression, such as hormone variation, show extensive flexibility over evolutionary time in their association with aggression (Hau, 2007; Wingfield et al., 2007). For example, aggression is closely linked to testosterone levels in males of many temperate songbird species but is very low and not responsive to territorial challenges in tropical species (Wingfield et al., 2007). Moreover, many bird species that are territorial in the nonbreeding season when gonads are regressed (reduced in size and nonfunctional) also show dissociation between testosterone and aggression (e.g., Schwabl & Kriner, 1991; Soma et al., 2000). Finally, in a recent study, there was no correlation between testosterone levels and aggressive personality differences in western bluebirds (*Sialia mexicana*) (Duckworth & Sockman, 2012). These studies suggest that the association between testosterone and aggression is flexible over an evolutionarily timescale and that endocrine responsiveness in adulthood is not likely to be an important constraint on the evolution of behavioral flexibility. However, hormones may still act during early development to influence aggressive personality as recent research on both humans and model lab organisms has demonstrated a link between personality variation and hormone exposure early in ontogeny (Carere & Balthazart, 2007; Hines, 2008). In sum, more work is necessary to understand how natural selection shapes aggression and how individual differences in aggression develop in order to understand why consistent differences in aggression are so common across a wide variety of animal species.

EVOLUTION OF CORRELATIONS BETWEEN AGGRESSION AND OTHER TRAITS

Individuals vary in morphological, behavioral, and life history traits that influence the costs and benefits of aggressive behavior either through functional links or through trade-offs. Thus, associations between other traits and aggression can evolve if selection favors their coexpression. Once formed, correlations between traits can constrain their independent evolution and can significantly affect each trait's future response to selection (Riska, 1989; Roff, 1997; Lynch & Walsh, 1998). In this section, I will review evidence for associations between aggression and other traits such as body size, dominance, parental care, and other personality traits as these are the traits most commonly predicted to be linked to aggression. I will also discuss the implications of these correlations for understanding the function and evolution of aggression and the extent to which these correlations might constrain adaptive evolution of aggression.

Body Size and Aggression

Body size and aggression are often functionally linked because the costs of initiating an aggressive encounter are less for larger compared to smaller animals. Moreover, differences in aggression can cause differences in body size. For example, in the desert spider (*Agelenopsis aperta*), more aggressive individuals are better foragers and thus reach a larger body size because of their ability to acquire more food (Riechert & Johns, 2003). These clear functional links between aggression and body size have led to the general prediction of a positive correlation between aggression and body size; however, even though larger individuals are more aggressive in some species (e.g., Zack, 1975; Brace & Pavey, 1978; Dowds & Elwood, 1985; Herrel et al., 2009), in many other species aggression and body size are either unlinked or smaller individuals are more aggressive (Just & Morris, 2003; Morrell et al., 2005). For example, in two species of swordtail fishes (*Xiphophorus nigrensis* and *X. multilineatus*), when the difference in size between fish was very large, contests were settled without fights and the smaller animal retreated; however, when individuals were more closely matched in size, 78 percent of observed fights were initiated by the smaller individual, and in 70 percent of the fights, the fish that attacked first lost the contest because body size was a better predictor of winning than aggression (Morris et al., 1995). In a recent study of zebra finches (*Taeniopygia guttata*), aggression was only weakly correlated with body size, and this relationship differed among the sexes such that the two traits were positively correlated in males and negatively correlated in females (Bolund et al., 2007). In more than 50 percent of staged interactions between velvet swimming crabs (*Necora puber*), aggression was initiated by the smaller crab, even though it was less likely to win (Smith et al., 1994). Finally, in western bluebirds, aggression and body size are not correlated, and moreover, western bluebirds, even though smaller than their sister species mountain bluebirds (*S. currucoides*), are more aggressive and are competitively superior to them in territorial disputes (Duckworth & Badyaev, 2007). Thus, the main theme that emerges from a review of studies measuring the relationship between body size and aggression is that there is no consistent pattern across species in the association of these traits.

The lack of a reliable relationship between aggression and body size suggests that there is no consistent strategy that large and small animals pursue in conflict situations. In fact, the only consistent pattern that emerges is that fights usually do not occur when individuals are extremely different in body size as visual cues apparently provide adequate information about competitive differences such that individuals do not need to fight to determine dominance.

Dominance and Aggression

Dominance refers to a status of power of one individual over another individual, whereas aggression refers to a specific set of behaviors such as attacks, chases, or displacements that are elicited with an intent to inflict harm on or instill fear into another individual. Dominance relationships are often assessed by observing agonistic interactions between individuals and determining which one relents. Dominance and aggression are so intricately linked that many studies use the terms interchangeably (Drews, 1993). While aggression and dominance are frequently correlated (e.g., Anestis, 2005; Colléter & Brown, 2011; Riebli et al., 2011), there are many exceptions. For example, in pronghorn antelope (*Antilocapra americana*), bank voles (*Myodes glareolus*), and domestic pigs (*Sus scrofa*), aggressive personality and dominance status are unrelated (Fairbanks, 1994; Bolhuis et al., 2005; Korpela et al., 2011). Moreover, Richard Francis (1983) showed that in paradise fish (*Macropodus opercularis*), males that were generally dominant across multiple encounters did not differ in their aggressiveness from males that were generally submissive. In fact, after subjecting paradise fish to five generations of bidirectional selection for dominance, he showed that even though the lines diverged significantly in their dominance by the end of the experiment, they did not differ in aggression (Figure 10.3). Wolves (*Canus lupus*) provide another illustrative example. Despite the prevailing view that a wolf pack is a group of individuals aggressively vying for dominance, in naturally occurring wolf packs aggression is rarely used to establish dominance (Mech, 1999). In fact, in one free-living pack observed over a 13-year period, no aggressive interactions were ever observed (Mech, 1999). This example appears to characterize the majority of wild pack behavior as the typical wolf pack is a family and the breeding pair is able to maintain its status without aggression. Submissive behavior, rather than being a response to aggression, is performed by the offspring toward the breeding pair or occasionally by the breeding female to the breeding male. In the wild, only larger packs including nonkin show aggressive behavior (Bradshaw et al., 2009).

To explain the lack of a general relationship between dominance and aggression, Francis (1988) put forward an intriguing possibility—that dominance status is not related to individual differences in aggression despite the fact that dominance relationships are often established through use of aggressive behavior. To understand this perspective it is important to distinguish between measurements of an individual's overall level of aggressiveness outside the context of a specific dominance interaction and what individuals actually do during a dominance interaction. In other words, even though dominant
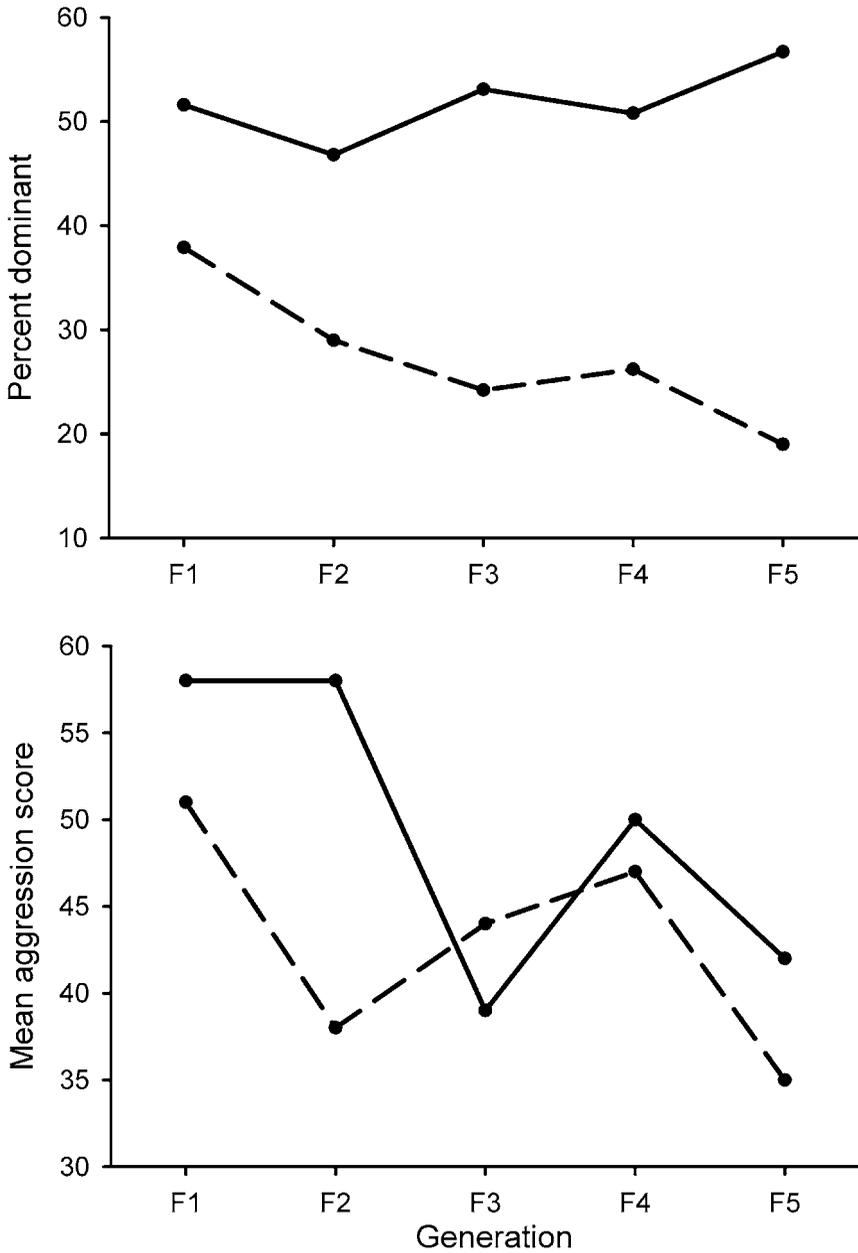
Figure 10.3. Divergent selection lines. Artificial selection experiments are a tool frequently used by evolutionary biologists to gain insight into the genetics of trait variation. These experiments start with a group of individuals that vary in the trait of

interest. "High" and "low" selection lines are created from this initial group by selecting only individuals that display either the highest or lowest expression of the focal trait to reproduce (e.g., only individuals in the top or bottom 25 percent of trait values are selected for breeding). These experiments can provide insight into many aspects of the genetics of a trait, including the symmetry of response to upward and downward selection (Pitnick & Miller, 2000) and whether there are correlated responses in other traits to selection on the focal trait (Schwarzkopf et al., 1999). Correlated responses are commonly caused by pleiotropy, in which one gene affects more than one trait. Thus, artificial selection experiments can shed light on how traits are linked. In a study by Francis (1984), an artificial selection experiment was carried out in paradise fish (*Macropodus opercularis*) for five generations. Both high and low lines for dominance were created where only individuals ranking in the top and bottom ~20 percent in dominance status were selected to breed. The results showed a significant response to selection in the downward but not the upward selected lines (top graph). However, when the same selection lines were tested for aggression by exposing them to an intruder fish (either another male separated by a glass partition or a mirror), they showed no difference in aggression from one another (bottom graph). This experiment showed that divergence in the dominance scores of the two lines was not accompanied by any changes in aggressiveness, showing that these traits are not linked in this species. (Figures adapted from Francis, 1984)

individuals may occasionally use aggression to establish or maintain dominance, this does not mean that they are generally more aggressive than other individuals.

If aggression plays only a limited role, then *what factors are most important in influencing dominance*? Dominance is an emergent property influenced by multiple interacting factors including both intrinsic characteristics of the individual as well as social context (Weiß et al., 2011). Intrinsic characteristics include differences in sex, body size, motivation, prior experience, age, and sexual traits (e.g., Watt, 1986; Lemel & Wallin, 1993; Elwood et al., 1998; Nosil, 2002; Duckworth et al., 2004). In general, males are dominant to females, larger individuals are dominant to smaller ones; older, more experienced individuals are dominant to younger, less experienced ones; and motivation can overturn any of these generalities (Cristol, 1992; Lemel & Wallin, 1993), especially if there is a large difference between individuals in the benefits of accessing a particular resource (Enquist & Leimar, 1987). For example, in house crickets (*Acheta domesticus*), body size usually determines the outcome of dominance interactions; however, when motivation is maximized by food deprivation, this overrides the effects of male body size (Nosil, 2002).

Furthermore, in natural populations of birds, the effects of motivation have been shown to be an important determinant of dominance even in species where, all else being equal, the largest or most ornamented males win contests (Lemel & Wallin, 1993).

Recently, a more nuanced view of aggression's relation to dominance is emerging where it is less important in establishing long-term dominance relationships and instead is more important for short-term or initial interactions between individuals. Support for this idea comes from studies of aggression in primate species. Multiple experiments that attempted to elicit aggressive interactions from stable primate groups in captivity (e.g., by making food or space more scarce) failed (Bernstein & Gordon, 1974). The only predictable trigger of aggression occurred when a foreign individual or individuals were introduced into a stable group. Typically, the intruding animal was severely attacked, but initial high levels of aggression declined rapidly, especially when the intruding animal behaved submissively, suggesting that aggression was motivated primarily by the need to maintain social order rather than as a means for mediating competition for resources (Bernstein & Gordon, 1974; de Waal, 1986). In domestic cats (*Felis catus*), dominance sustained without the use of aggression was more stable than dominance formed on the basis of aggressive display (Fonberg, 1988). Many studies of birds have shown that once individuals get to know each other well, they do not use aggression to maintain dominance (Temeles, 1994). Finally, in *Chasmognathus* crabs, Silvia Pedetta and colleagues found that aggression is the main determinant of dominance between size-matched individuals (Pedetta et al., 2010). In fact, aggression even overrides prior experience in this species—in lab trials, even when pitting the same individuals against one another multiple times, the crabs fight anew, and there seems to be no memory of previous encounters. They suggest this makes sense in the context of this species's natural history as interactions with conspecifics occur mainly in the context of burrow disputes between resident and wandering crabs, and it is rare that fights would occur between the same opponents multiple times. Thus, there is no benefit for **individual recognition** mechanisms to evolve in this species. These studies all suggest that aggression may be more important for short-term or one-time interactions and less of a factor for maintaining long-term dominance hierarchies. The implications are that it may be important to understand the expected duration of conflict situations in order to understand when and why individual variation in aggression evolves.

Parental Care and Aggression

Aggression is costly in terms of time, energy, and risk, and thus is expected to trade off with investment in other costly behaviors and traits (Bennett

& Houck, 1983; Robertson, 1986; Johnstone & Norris, 1993; Duckworth, 2006a; Rosvall, 2011). In fact, one of the most consistent relationships between aggression and other traits across a wide variety of species is a negative correlation between aggression and *parental care*. For example, in many passerine birds, males that show high levels of aggression often invest the least in parental care (Ketterson & Nolan, 1994). Because, in these species, males and females form strong pair bonds and both sexes contribute to offspring care, this means that highly aggressive males often have lower reproductive success (e.g., Duckworth, 2006a). In some of these species, variation in aggression is related to alternative male mating strategies within a population, where aggressive males compensate for fitness costs of low parental care by actively pursuing mating opportunities outside the pair bond, whereas other males are nonaggressive and good fathers (Ketterson & Nolan, 1994). Why aggression, mating behavior, and parental care are frequently linked is not clear. It is known that all of these behaviors are influenced by circulating testosterone levels—testosterone is necessary for sperm production and hence mating, frequently correlates with aggression, and is antagonistic to the expression of parental behavior. These links have led to the idea that negative correlations between aggression and parental care are primarily due to the joint effects of testosterone. However, whether aggression and parental behavior are linked directly or whether they are instead only correlated through testosterone is still an open question. If the latter, then in species where testosterone and aggression are uncoupled, there should not be a trade-off between aggression and parental behavior. Direct links between aggression and parental care could occur if there is a fundamental neural trade-off where individuals "wired" to be aggressive cannot also be parental, and vice versa. Finally, it is also possible that there is a basic time or energy trade-off that links these two behaviors such that aggressive individuals spend so much time fighting they do not have time or energy left for offspring care.

Recent studies suggest that the relationship between aggression and parental behavior may be more complex than originally thought and that the antagonistic effects of testosterone on parental behavior may not always be present (see Lynn, 2008, for review). For example, in western bluebirds, aggressive personality differences are unrelated to natural variation in testosterone even though there is a negative relationship between aggression and male parental care in this species (Duckworth, 2006a; Duckworth & Sockman 2012). Moreover, in California mice (*Peromyscus californicus*), testosterone is actually required to maintain high levels of paternal behavior, paternal behavior and aggression are positively correlated, and testosterone and aggression are not related in a simple way (Trainor & Marler, 2001). Both castration and

experimentally increased testosterone did not influence aggressive response in this species; instead only the control males increased their aggression in response to a social challenge. The authors suggest that this counterintuitive result may be because this was the only group whose level of aggression was allowed to fluctuate naturally, suggesting that testosterone responsiveness to social challenge, rather than mean level of testosterone, may be more important in modulating aggressiveness in this species. Finally, even in many bird species, recent studies are showing that some species are "behaviorally insensitive" to testosterone such that experimental increases in testosterone do not increase aggressive behavior and fail to dampen parental behaviors (Lynn, 2008). Thus, taken together, these studies show that testosterone does not universally mediate the trade-off between aggression and parental care across species. Moreover, this relationship was mainly developed in songbirds, and, as shown by the California mice example, more evidence is needed from a broader array of taxa to determine whether the trade-off between aggression and parental care is universal.

Temperament Traits and Aggression

In a recent review, Denis Réale and colleagues characterized aggressiveness as one of five temperament (or personality) categories that also include shyness-boldness, exploration-avoidance, activity, and sociability (Réale et al. 2007). Correlations among these distinct behavioral axes are widespread and are referred to as **behavioral syndromes** (Sih et al., 2004). Many studies have documented an aggression-boldness syndrome—where animals that are more aggressive are also bolder and more explorative in novel environments (first described by Huntingford, 1976; see Norton et al., 2011, and citations therein for examples). Although correlations between these personality axes are common, they are not ubiquitous and appear to be maintained by natural selection. For example, in threespine sticklebacks (*Gasterosteus aculeatus*) the presence of this behavioral syndrome is correlated with predation pressure across populations such that in populations with high predation the correlation between boldness and aggression is strong, but it breaks down in populations with less intense predation (Bell & Stamps, 2004; Dingemanse et al., 2007). As an adaptive explanation for such a pattern, Niels Dingemanse and colleagues suggested that in ponds with predators, spatial variation in predation risk might favor evolution of alternative solitary or shoaling strategies where solitary individuals monopolize a habitat patch that is poor in food but safe and shoaling individuals roam patches of habitat that are relatively dangerous but rich in food (Dingemanse et al., 2007). Competition for safe patches would be intense, and so solitary individuals should be aggressive

and also more exploratory because they have to find patches on their own, whereas shoaling individuals need to be more tolerant of neighbors and can also rely on them to acquire foraging information, so they do not need to be as explorative.

Such adaptive explanations for correlations between aggression and exploratory behavior still need to be tested, but trade-offs originating from differences in social strategy might be the key to understanding correlations between personality traits as these correlations are often found in species where there is wide variation in social strategy between individuals (Cote & Clobert, 2007; Bergmüller & Taborsky, 2010). Examples include freshwater fish, where solitary individuals are both more explorative and aggressive than social individuals (Ward et al., 2004); *Myrmica* ants, where there are strong correlations between aggression, boldness, activity, and sociability at the individual, caste, and colony levels (Chapman et al., 2011); the cooperatively breeding cichlid (*Neolamprologus pulcher*), where an aggression-boldness-explorativeness syndrome was linked to female helping behavior (Schürch & Heg, 2010); and the socially polymorphic comb-footed spider (*Anelosimus studiosus*), where social individuals were less aggressive, less active, and less responsive to prey (Pruitt et al., 2008). Social conflict can select for stable coexistence of different behavioral types, and this has led to the idea that personality differences may evolve primarily in response to social environment (Bergmüller & Taborsky, 2010). While this is an intriguing idea, the evidence so far is only correlative, and the direction of causality between different personality axes is not clear. After all, differences in aggression between individuals might be as likely to lead to differences in sociability as the reverse.

Correlations between Aggression and Other Traits: Ever-present, but Not Consistent

Two main themes emerge from a survey of correlations between aggression and other traits: (1) such correlations are widespread across a diverse array of taxa and (2) there are no consistent patterns across taxa in the specific traits that are correlated with aggression. Aggression is closely linked to body size and dominance in some species but not others. It frequently covaries with aspects of life history investment, such as parental care, but not consistently across species. Many species show strong correlations between aggression and other components of personality variation, but the strength and presence of these correlations vary across species and even across populations within a species.

Such diversity in the strength and direction of correlations has important implications for understanding the evolution of distinct aggressive phenotypes. First, it reinforces the importance of aggression in a wide variety of contexts

and life histories. Second, it suggests that the evolution of aggression is not constrained by correlations with other traits, as these correlations can break up and be reformed in a relatively short time span (~10,000 years in the case of stickleback populations that differ in the expression of behavioral correlations; Dingemanse et al., 2007). Finally, it supports the notion that aggression, rather than being an emergent property of other components of the phenotype, is a trait in its own right. After all, if aggression was always consistently correlated with other traits such as boldness or activity levels, this could indicate that these are not really separate traits at all but simply the distinct responses reflecting a common underlying temperament or coping style. In the next two sections, I discuss how individual, population, and species differences in aggression can influence ecological and evolutionary processes and how ecological and evolutionary feedbacks on aggression might provide the key to understanding both the diversity and ubiquity of correlations between aggression and other traits.

ECOLOGICAL CONSEQUENCES OF AGGRESSION

There is a long history of research that investigates the role of aggressive interactions in population and community ecology (Walls, 1990; Amarasekare, 2002; Peiman & Robinson, 2010). By directly affecting competitive interactions between individuals, variation in aggression can influence individual spacing patterns, population dynamics, and population cycles. Moreover, recent studies have found links between aggression and dispersal behavior (e.g., Rusu & Krackow, 2005; Duckworth & Badyaev, 2007; Raihani et al., 2008). Thus, aggression may also influence population connectivity and the dynamics of colonization. In fact, recent studies have indicated that distinct aggressive phenotypes may play a role in species range expansions as well as the success of invasive species. In this section, I will review the evidence that variation in aggressive behavior has strong impacts on ecological dynamics.

Aggression, Individual Spacing, and Population Cycles

In territorial species, aggression can influence individual spacing, which in turn can have large effects on population density and potentially even population cycles (Adams, 2001). One of the earliest proponents of linking aggression to population cycles was Dennis Chitty (1952), who suggested that at high density selection favors large, aggressive animals with low reproductive rates, and at low densities it favors smaller, less aggressive animals with high reproductive rates (Chitty, 1967). Subsequent researchers expanded on these ideas to take into account the potential role of kin interactions (Charnov & Finerty, 1980). However, experimental tests of these ideas have not held up

in cycling populations of microtine voles (Boonstra & Hogg, 1988; Boonstra et al., 1994), leading to the conclusion that intrinsic changes in behavior alone could not account for populations cycles (Stenseth & Łomnicki, 1990; Stenseth et al., 1996).

Recent work in birds has shown that, in conjunction with extrinsic factors, aggression can play a key role in population cycles. In red grouse (*Lagopus lagopus scoticus*), there has long been a debate about the relative importance of intrinsic changes in aggression versus extrinsic fluctuations in parasite loads in driving population cycles. While experimental studies have shown that changes in parasitism can produce cycles through their effects on breeding productivity (Hudson, 1986), there is also strong evidence that population cycles are caused by annual variation in the aggressiveness of males through its effects on populations density and recruitment of new individuals into the population (Mougeot et al., 2003). Researchers were able to mimic population cycles in a Scottish population by experimentally increasing aggressiveness with testosterone implants in four separate populations. As aggression increased, males expanded their territories and recruitment of new males into the population declined, resulting in a breeding density that was reduced by 50 percent, changing the populations' trajectories from increasing to declining. However, while the effects of aggression on population cycles were clear, it was not clear what ultimately drove changes in aggression. Subsequent studies showed that high levels of testosterone increased parasite infection, which in turn decreased male aggressive behavior (Fox & Hudson, 2001; Seivwright et al., 2005). Thus, the most recent consensus suggests that a combination of extrinsic fluctuations in parasite loads and intrinsic fluctuations in aggression are necessary to explain the observed population cycles (New et al., 2009).

Aggression is also linked to population density and population cycles in bluebirds (*Sialia* spp.). Western bluebirds depend on tree cavities to breed— a limiting resource that historically was patchily distributed and ephemeral. Nest cavities occur at high densities following forest fires, which create suitable habitats for bluebirds by opening up understory vegetation and creating dead snags where nest holes are abundant. Eventually, as the forest regrows, bluebirds are no longer able to breed in these habitat patches because snag density decreases and regrowth of the forest eliminates the open meadows bluebirds depend on to forage for insect prey (Power & Lombardo, 1996; Guinan et al., 2000). Western bluebirds' sister species, mountain bluebirds, are frequently among the earliest colonizers following forest fires (Hutto, 1995), whereas, western bluebirds often show delayed patterns of colonization (Saab et al., 2004; Kotliar et al., 2007). Competition for nest cavities among these and other secondary-cavity-nesting species is intense and often involves

aggressive displacement (Gowaty, 1984; Newton, 1994; Merilä & Wiggins, 1995). Western bluebirds, while less dispersive and slower to find new habitat, are on average more aggressive than mountain bluebirds and rapidly displace them when they colonize new areas (Duckworth & Badyaev, 2007). The maintenance of these cycles of species replacement depends at least partly on the evolution of two distinct dispersal strategies in western bluebirds in which dispersal and aggression are closely linked. Highly aggressive males tend to leave their natal populations and disperse to new areas to breed—these newly colonized areas initially have a very low population density, and this enables aggressive males to obtain large territories. On the other hand, nonaggressive males tend to remain near where they were born, which usually has a much older population with a higher density of western bluebirds than newly colonized areas (Duckworth & Badyaev, 2007; Duckworth, 2008). These patterns of biased dispersal with respect to aggression produce a strong correlation between population age, density, and aggressive behavior. Newly colonized population are less dense but highly aggressive, whereas older, well-established populations are less aggressive and have higher densities.

These avian examples show that aggression can be an important determinant of population cycles, however, not in the ways originally envisioned by Chitty (1967)—body size and aggression are not linked in these species, and in both examples, aggression was associated with lower population density because more aggressive individuals are more likely to space themselves farther apart and social tolerance among related individuals enables them to breed at higher density (Lambin & Krebs, 1991). It remains to be seen whether cycles of aggression might play an important role in other classic systems that show populations cycles, such as snowshoe hares (*Lepus americanus*) and the Norway lemming (*Lemmus lemmus*).

Aggression, Invasion, and Range Limits

Recent studies have linked differences in aggression between populations and species to the dynamics of invasion and range expansion. The Argentine ant (*Linepithema humile*) is an invasive species whose success has been attributed at least in part to its aggressive displacement of other species. Introduced populations have undergone ***genetic bottlenecks*** that have led to very low genetic diversity and the growth of "super-colonies" with nests that essentially function as a single colony spread over many kilometers (Suarez et al., 2008). Nests within these super-colonies are not aggressive toward one another due to their genetic similarity but are very aggressive to other species. In contrast, in the native range, Argentine ants do not form such super-colonies, display

much higher levels of intraspecific aggression, and coexist with a diverse community of ant species. These patterns suggest that changes in colony structure and aggression in introduced populations have facilitated invasion success by decreasing intraspecific competition and thus enabling them to outcompete other species (Holway, 1999; Tsutsui et al., 2003). Finally, the red-eared slider (*Trachemys scripta elegans*) and endangered native Spanish terrapin (*Mauremys leprosa*) in the Iberian Peninsula provide another example linking aggression and invasiveness. Red-eared sliders are more aggressive than Spanish terrapins and outcompete them during foraging, significantly restricting their access to food resources (Polo-Cavia et al., 2011).

Aggressive differences between species are not just linked to successful invasions but have also been shown to be important in the dynamics of natural range expansions and in determining species' range limits (Peiman & Robinson, 2010). Scott Pearson and Sievert Rowher (2000) found that competitive superiority of Townsend's warblers (*Dendroica townsendi*) over hermit warblers (*D. occidentalis*) is causing the hybrid zone to move in these species, thereby expanding Townsend's warblers' range at the expense of hermit warblers. They showed that this competitive difference between the species was largely attributable to differences in aggression—Townsend's warblers are more aggressive than hermit warblers. Similarly, the recent range expansion of the barred owl (*Strix varia*) at the expense of the threatened northern spotted owl is at least partly due to its higher aggression (Van Lanen et al., 2011). In bluebirds, competitive superiority of western bluebirds over mountain bluebirds is largely due to the highly aggressive nature of western bluebirds that colonize new populations (Duckworth, 2008). This competitive difference was most obvious during western bluebirds' recent range expansion, in which nest-box programs enabled them to rapidly recolonize areas in the northwestern United States where they had originally gone extinct due to the loss of natural nest cavities. The expansion of their range back to their historical range limits was accompanied by the rapid displacement of lower-elevation mountain bluebird populations (Duckworth & Badyaev, 2007). Interestingly, the range expansion was a natural experiment that provided insight into the competitive dynamics of these species—it showed that mountain bluebirds are limited at the lower edge of their range by competition with western bluebirds rather than by abiotic or other ecological factors.

Such competitive exclusion through direct aggressive interactions is a common theme, especially in the context of species range limits across elevational gradients. In two tropical bird genera—*Catharus* thrushes and *Henicorhina* wrens—asymmetries in aggressiveness explained nonoverlapping ranges across an elevational gradient in tropical forests (Jankowski et al., 2010).

Differences in aggression among four *Eutamias* chipmunks occurring across an elevational gradient in the Sierra Nevada Mountains is thought to at least partially explain their nonoverlapping distributions (Heller, 1971). In *Plethodon* salamanders, evidence suggests that high levels of interspecific aggression have evolved in populations in the Great Smoky Mountains, causing elevational range segregation between *P. glutinosus* and *P. jordani*, whereas in the Balsam Mountains interspecific aggression was largely absent and the two species' ranges overlapped extensively (Hairston et al., 1987). One pattern that emerges across these studies is that the more aggressive species usually lives in the more mild ecological conditions. This pattern is not confined to elevational gradients—red foxes (*Vulpes vulpes*; Figure 10.4) are more aggressive then and competitively dominant to arctic foxes (*Alopex lagopus*) (Frafjord et al., 1989). Evidence suggests that the arctic fox is limited at its southern range edge by the more aggressive red fox and the red fox is limited at its northern range edge by its inability to cope with the extreme climactic conditions of the arctic (Hersteinsson & MacDonald, 1992; Tannerfeldt et al., 2002).

Figure 10.4.   Red foxes (*Vulpes vulpes*) fighting. Red foxes are more aggressive than arctic foxes (*Vulpes lagopus*), and their competitive superiority may be at least partly responsible for declining arctic fox populations in Scandinavia. (Alex Badyaev, www.tenbestphotos.com)

Thus, high levels of aggression may be necessary to exclude competitors from areas of abundant resources but may come at the cost of surviving and breeding in more extreme ecological conditions.

EVOLUTIONARY CONSEQUENCES OF AGGRESSION

Strong ecological consequences of aggressive interactions can affect future evolutionary trajectory of populations. Aggressive behavior has great potential to affect selection pressures because it is often used to obtain a breeding territory (Stamps & Krishnan, 1997) and therefore can affect individual fitness by determining the quality of environment in which offspring develop. Western bluebirds provide one of the clearest examples of territorial aggression influencing natural selection. As secondary cavity nesters, their nest sites are extremely limited, and as a consequence, males prefer to acquire territories with multiple nest cavities (Meek & Robertson, 1991; Plissner & Gowaty, 1995); however, only the most aggressive males are able to compete successfully for these territories (Duckworth, 2006b). Using this knowledge, I tested the idea that aggressive interactions over nest cavities could cause males to sort into distinct habitats, which in turn could influence evolution of morphology (Duckworth, 2006b). By placing a high density of nest boxes in open habitat with very low tree cover and a low density of nest boxes in closed habitat with high tree cover, I experimentally caused aggressive interactions to sort males into these different habitats. Aggressive males acquired territories with multiple nest boxes in the open habitat, and nonaggressive males were pushed into the closed habitat where they acquired territories with only a single nest box. Most importantly, males experienced differential selection on morphology across these habitat types. Specifically, males with longer tails and legs were favored in open habitats where high agility is required to forage efficiently, whereas in forested habitats, where agility is less important, selection on morphology was weak. These results showed that aggression can affect selection on a local scale by determining individual settlement patterns. Moreover, because such sorting caused a correlation between aggression and selection on body size, this study has important implications for our understanding of how correlations between aggression and other traits might originate—through a nonrandom link between aggression and habitat type.

Aggressive interactions between species can also have evolutionary consequences through ***agonistic character displacement*** (Grether et al., 2009). Classic ***character displacement*** occurs when competition between species causes them to diverge in traits in populations where their ranges overlap compared to populations where their ranges do not overlap (Grant, 1994). Such

divergence is thought to lessen interspecific competition and enable coexistence in areas of overlap. Agonistic character displacement is a specialized case where divergence in areas of overlap occurs specifically in traits that affect the rate, intensity, or outcome of competitive interactions. One of the clearest examples of such agonistic character displacement is the case of brook and ninespine sticklebacks (*Culaea inconstans* and *Pungitius pungitius*, respectively). Kathryn Peiman and Beren Robinson (2007) showed that brook sticklebacks from populations that overlap with ninespine sticklebacks are more aggressive than those from populations that do not overlap, suggesting that there has been selection for enhanced aggressiveness where these species come into contact. In another example, Dean Adams (2004) found that robustness of head shape—a trait that is associated with enhanced fighting ability—showed increases in areas of overlap for two *Plethodon* salamanders, *P. jordani* and *P. teyahalee*. Moreover, he found a positive correlation between head shape and aggression. He suggested that these differences in head shape stemmed from aggressive interference competition— salamanders that were more aggressive benefited from having a morphology that increased their fighting ability.

The outcome of aggressive interactions will depend not only on an individual's own aggressive behavior but also on the aggressive phenotype of other individuals in the population. This social context of aggression can produce novel evolutionary feedback dynamics for aggression and the traits associated with aggression, particularly because the environment that elicits aggression (other competitors) can evolve. Such influences of genotypes of other individuals in the population on a focal individual's aggression are termed ***indirect genetic effects*** (Wolf et al., 1998). The importance of indirect genetic effects for evolution have only recently been recognized. In one of the few empirical papers showing indirect genetic effects on aggression, Alastair Wilson and colleagues (2009) found a strong positive ***genetic covariance*** between a focal individual's aggression and the aggression of its opponent. Such covariance between aggression and the social environment can lead to positive evolutionary feedbacks and result in rapid evolution of aggression in the presence of strong natural selection (Wolf et al., 1998).

CONCLUSIONS

Animals display aggression in a wide range of circumstances from competition over mates, food, or other resources, to territory defense and offspring protection, to the establishment of dominance hierarchies within social groups. The ubiquity and importance of aggression has made it the focus of an immense amount of research, making studies of the evolution of aggression a rich resource for understanding the evolution of behavior more generally.

While early studies of aggression focused on trying to understand the optimal expression of aggression within a population (Maynard Smith & Price, 1973; Parker, 1974), recent studies showing consistent differences among individuals have shifted the focus to trying to understand the relative importance of selection and constraint in shaping aggressive phenotypes. These studies have shown that aggression is among the most repeatable of behavioral traits, often varies extensively among individuals within populations, and is frequently correlated with other behaviors. Selection for integration of aggression with other traits is often cited as a key component of adaptive hypotheses for the evolution of consistent individual differences, and while the ubiquity of correlations between aggression and other traits supports this idea, it is not clear whether consistent differences in aggression are a cause or consequence of these correlations. Certainly, the diversity of correlations between aggression and other traits suggests that, if selection for integration is the main cause, then there is a diversity of ways for selection to produce consistent individual differences in aggression. At the same time, the idea that developmental constraints play an important role in the evolution of constancy in the expression of aggression needs empirical testing. Under the constraint hypothesis, correlations between aggression and other traits might be a consequence of consistent differences rather than a cause. More work on the patterns of trait correlations as well as the developmental basis for differences in aggression across a diversity of species is needed to test these alternative hypotheses.

Finally, individual, population-, and species-level variations in aggression can have large-scale ecological consequences by influencing population density and species coexistence. Recent studies show that distinct aggressive phenotypes play a role in population cycles, range expansions, and the success of invasive species as well as competitive exclusion at range edges. In turn, these strong ecological consequences of aggressive interactions can influence evolutionary dynamics of populations, ultimately producing feedbacks that further influence the evolution of aggression.

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