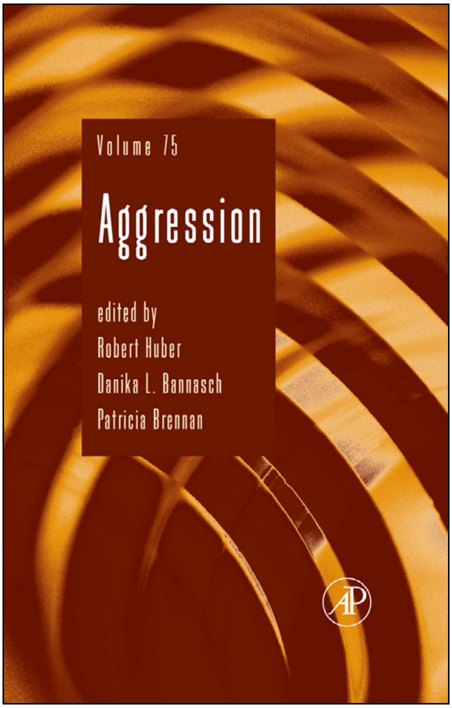

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Signaling Aggression

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ABSTRACT

From psychological and sociological standpoints, aggression is regarded as intentional behavior aimed at inflicting pain and manifested by hostility and attacking behaviors. In contrast, biologists define aggression as behavior associated with attack or escalation toward attack, omitting any stipulation about intentions and goals. Certain animal signals are strongly associated with escalation toward attack and have the same function as physical attack in intimidating opponents and winning contests, and ethologists therefore consider them an integral part of aggressive behavior. Aggressive signals have been molded by evolution to make them ever more effective in mediating interactions between the contestants. Early theoretical analyses of aggressive signaling suggested that signals could never be honest about fighting ability or aggressive intentions because weak individuals would exaggerate such signals whenever they were effective in influencing the behavior of opponents. More recent game theory models, however, demonstrate that given the right costs and constraints, aggressive signals are both reliable about strength and intentions and effective in influencing contest outcomes. Here, we review the role of signaling in lieu of physical violence, considering threat displays from an ethological perspective as an adaptive outcome of evolutionary selection pressures. Fighting prowess is conveyed by performance signals whose production is constrained by physical ability and thus limited to just some individuals, whereas aggressive intent is encoded in strategic signals that all signalers are able to produce. We illustrate recent advances in the study of aggressive signaling with case studies of charismatic taxa that employ a range of sensory modalities, viz. visual and chemical signaling in cephalopod behavior, and indicators of aggressive intent in the territorial calls of songbirds.

I. INTRODUCTION

Although physical fighting, including the killing of conspecifics, is widespread in nonhuman animals just as it is in humans, the majority of contests and disputes in nonhuman animals are settled without physical fighting. Rather than resorting to immediate physical combat, nonhuman animals often engage instead in extended bouts of signaling, making prominent display of their weapons (e.g., antlers, claws, and teeth), or running through a repertoire of highly stereotyped agonistic signals. With their high cognitive capacity, primates (humans included) are particularly good at reducing social tensions and resolving conflicts using agonistic signaling as opposed to sheer physical force (Cheney *et al.*, 1986).

Such aggressive signaling is found in virtually all of the multicellular taxa and can involve all communication modalities. Orthoptera (Alexander, 1961; Simmonds and Bailey, 1993) and many other insects (Clark and Moore, 1995; Jonsson *et al.*, 2011) use aggressive song to defend resources, and the use of territorial song in birds is well known (Searcy and Yasukawa, 1990; Stoddard *et al.*, 1988). Calls are employed to similar effect in the dramatic displays of large mammals or frog choruses (Bee *et al.*, 1999; Reby *et al.*, 2005; Wagner, 1992), and more subtly by other vertebrate taxa such as fish (Raffinger and Ladich, 2009). In these scenarios, signaling can be just as effective as physical attack in intimidating opponents and winning contested resources.

Chemical signals are widely used to signal resource defense and fighting ability, deposited either as scent marks in fixed locales by terrestrial species (Page and Jaeger, 2004) or contained in urine released during aggressive interactions in some aquatic organisms (Breithaupt and Eger, 2002). Visual signals are perhaps the most familiar and easily appreciated of aggressive displays, beginning with Darwin's (1871) graphic illustration of aggression and fear in the facial expression of the domestic dog. Visual signs of aggression include variable pigment patterns of many fish and cephalopods (DiMarco and Hanlon, 1997; Moretz and Morris, 2003), and the ritualized display of weapons (Huber and Kravitz, 1995; Lundrigan, 1996) or inedible objects as "props" (Murphy, 2008).

Phylogenetic comparative analyses demonstrate that many of these aggressive signals allowing opponents to resolve contests without physical harm evolved from nonsignaling behaviors through the process of ritualization (Scott *et al.*, 2010; Turner *et al.*, 2007). Whereas agonistic behavior runs the gamut from passivity, defense, and escape to full conflict, here, we reserve the terms aggressive/threatening behavior for that subset of agonistic behavior associated with the escalation toward physical fighting (Searcy and Beecher, 2009).

A. An ethological approach to aggression

The ethological approach to aggression derives historically from the traditional instincts and drives articulated by Lorenz (1978). Although the simple psychohydraulic model of motivation underlying this view proved inadequate in the long term, the idea that aggression is based on both internal state and external stimuli, and the proposed value of a comparative evolutionary approach, were both far-sighted and enduring. The classic *On Aggression* (Lorenz, 1963) which was written for a popular audience, highlighted aggression as a natural, evolved function, with a founding basis in other instincts, and a central role in animal communication. A more nuanced view is found in his work known as the Russian manuscript (Lorenz, 1995). In this, Lorenz discussed animals and humans separately, not because of any fundamental difference in their biology, but because he believed it necessary for the reader to have an adequate frame of reference.

Much current research on the biology of aggression focuses on identifying the physiological substrate to violence (i.e., on proximate cause and non-adaptive features). The ethological or sociobiological approach, in contrast, focuses attention on the ultimate causes and *adaptive* forms of aggressive behavior (e.g., Chen *et al.*, 2002; Huber and Kravitz, 1995; Miczek, *et al.*, 2007; Natarajan *et al.*, 2009): how and why has evolution molded complex agonistic interactions built on reciprocal displays of threat or submission, affect or intent?

B. The classic game theory model

Evolutionary fitness is measured in terms of the number of offspring an individual produces over the course of its lifetime. In the evolutionary race to transmit their genes to the following generations at a higher frequency than that of their conspecifics, these individuals must compete for access to all the resources necessary to create and raise their progeny, including mates, dominance rights, and desirable territory. Winners in this intraspecific competition thus stand to gain both immediate personal advantages such as food, space, and safety, as well as long-term evolutionary fitness, that is, more offspring and therefore copies of their genes in subsequent generations. Simulation approaches from game theory have long provided a theoretical framework for analyzing and predicting the outcomes of competitive interactions. The classic "*Hawks*" and "*Doves*" game (Maynard Smith and Price, 1973) considers symmetrical contests between pairs of individuals who are equivalent in every respect (equal size, strength, fighting ability, etc.), differing only in behavioral/fighting strategy in intraspecific encounters. *Hawk* strategists are those who will always choose to fight when they encounter a conspecific at a contested resource. *Dove* strategists, in contrast, always retreat from an individual behaving as a *Hawk*, rather than engage them in combat. *Hawks* always best *Doves*, but they incur costs when they compete against other *Hawks*. The outcome between two *Dove* strategists is randomly determined. Each conflict consists of a series of agonistic moves (incorporating provocation, escalation, retaliation, etc.) with rewards or costs assigned to each contestant according to a particular payoff matrix (Table 3.1).

Populations are expected to converge on an evolutionarily stable strategy (ESS), strategies that once they are predominant cannot be invaded by any other strategy. The ESS depends critically on the ratio of what an individual stands to gain over what it stands to lose in a fight. Thus, in the common situation where the cost of injury exceeds the benefits of winning, populations are expected to adjust to balanced proportions of the two strategies with the majority of individuals behaving as *Doves*, while a smaller number of *Hawk* strategists persists. Only in extreme situations where the value of a resource greatly exceeds the cost of injury, will a *Hawk* strategy be superior and can become so widespread as to completely replace the *Dove* strategy. For instance,

Table 3.1. The Payoff Matrix for the *Hawk–Dove* Game Shows the Consequences that Result When a Player of a Given Strategy (Left Column) Encounters Another Player's Strategy

	Hawk	*Dove*
Hawk	Tie [(V − C)/2]	Win [V]
Dove	Lose [0]	Tie [V/2]

Choices are assumed to be rational where each individual would prefer to win, prefer to tie rather than lose, and prefer to lose over receiving injury. In this payoff matrix, *V* (value of the contested resource) and C (cost of an escalated fight) determines the net outcome when different strategies meet. In encounters between *Hawks*, the winner gains control over the value of the resource while the losing *Hawk* sustains an injury. In the common scenario, where the value of the resource is less than the cost of injury (i.e., $C > V$), average payoff in a *Hawk* meeting a *Hawk* is negative and less than that of a *Dove* meeting a *Hawk*. Only in rare situations, when the value of the resource exceeds the cost of injury, will *Hawk* be unequivocally the superior strategy.

intense fighting among male elephant seals results in the victorious male both monopolizing a section of the beach and gaining sole reproductive access to the harem of females which resides there. In the vast majority of cases, however, resources are rarely worth the risk of injury, and competing individuals would do best to resolve conflicts via ritualized displays.

C. Signaling games

The earliest game theoretical analyses of aggressive signaling were pessimistic about the evolutionary stability of such systems (Caryl, 1979; Maynard Smith, 1974, 1979). Their reasoning was that if we assume that signals can help in winning contests by conveying high levels of aggression or fighting ability, then it becomes advantageous for all individuals to give the highest levels of these signals. If all individuals signal maximally, then there is no information in the signal about either aggressive intentions or fighting ability. The first rigorous game theoretical model to demonstrate that reliable aggressive signaling could be evolutionarily stable was a mutual signaling game in which two interactants chose between two cost-free signals to create a stable global strategy (Enquist, 1985). This model demonstrated how threat displays reveal information about the strength or condition of the contestants via their choice of action in aggressive encounters. The players in this game each have a hidden state (strength or weakness) which determines their ability to win physical fights. An honest weak individual gives a signal conveying weakness, and abandons the contest if the other individual gives a signal conveying strength. A dishonest weak individual can successfully bluff other weak individuals by giving the signal of strength, but at a cost of sometimes being attacked by a better fighter if the opponent turns out to be strong. If the cost of being attacked by a stronger individual is high relative to the benefit of winning contests, then bluffing may not be advantageous, and honest signaling can be evolutionarily stable.

There followed a slew of variant *Hawk/Dove* models which attempted to accommodate the diversity of interactions between senders and receivers (e.g., Enquist and Leimar, 1983; Leimar and Enquist, 1984; Maynard Smith and Harper, 1988; Skyrms, 2009). These models of communication may be classified into five structures based on the relative timing of the (signal and/or response) choices made by the two players during the game (reviewed in Hurd and Enquist, 2005). Mutual signaling games, which most closely resemble agonistic interactions between animals, are increasingly being used as models (e.g., Kim, 1995; Számadó, 2000). In this structure, both players signal, and react to their opponent's signal, in biologically realistic ways. Genetic algorithms are also being used to examine non-ESS solutions to these games (Hamblin and Hurd, 2007). Alternative approaches employ simulation methods and neural networks (Noble, 2000; Wheeler and de Bourcier, 1995) to explore communication in animal contests.

D. Threat displays and why they are part of aggression

Aggression is costly to participants not only in terms of energy expenditure and the potential for injury but also because of opportunity costs. Time spent in physical conflict is time that is not available for other vital activities such as exploring, feeding, or mating. Thus, there are selective advantages to reducing aggression. Threat displays are a critical component of aggression because they modulate competitive social interactions among conspecifics. If signaling is effectively delivered by a sender and appropriately interpreted by the intended receiver it might be so subtle that the interaction is rendered virtually invisible to an outside observer. Alternatively, if sender and receiver perceive the competitive difference between them to be slight, the social interaction is prolonged, escalates in intensity, and may ultimately culminate in levels of overt conflict that result in physical damage or death of one or both interactants.

In such aggressive signaling contests, two kinds of information are important to receivers: information on the signaler's willingness to escalate (aggressiveness motivation) and on its fighting ability (resource-holding potential) (Searcy and Beecher, 2009). Classification schemes based on the type of interaction in which communication takes place and the nature of the signals used converge on the following signal categories (Hurd and Enquist, 2005; Maynard Smith and Harper, 2003; Vehrencamp, 2000).

Performance signals are signals constrained to a subset of signalers either by differences in the ability to perform them (Maynard Smith, 1982), or by possessing the information needed to produce them (Hurd and Enquist, 2005).

Performance displays ("index signals" of Maynard Smith and Harper, 2003) have excellent empirical support, as do models of their use (e.g., Enquist and Leimar, 1983; Leimar and Enquist, 1984). Examples include the lateral displays of many fish (Enquist and Jakobsson, 1986) or the pitch of calls in many frog and mammal species (e.g., Bee *et al.*, 1999; Reby *et al.*, 2005), both "unfakeable" signals as they are determined by the sender's size and fighting ability.

Strategic signals are available to all signalers, and may be either *classic handicaps* or *conventional signals* (Hurd and Enquist, 2005). Classic handicaps have some inherent cost, independent of receiver response, and variation in the level of cost experienced by different individuals produces different optimum signaling levels (Grafen, 1990). Evidence for handicapped displays is theoretical (Zahavi, 1987) rather than empirical, though threat displays have been shown to advertise endurance in lizards (Brandt, 2002) and grasshoppers (Greenfield and Minckley, 1993). Conventional signals are arbitrary with respect to signal design and therefore dependent for meaning on an agreement between the signaler and receiver. Honesty of conventional signals in agonistic interactions is maintained by two forms of receiver-dependent stabilizing costs (Enquist, 1985; Guilford and Dawkins, 1995); receiver retaliation (Enquist, 1985) has empirical support (Molles and Vehrencamp, 2001) and vulnerability handicap (Zahavi, 1987) for which empirical support is contradictory (Laidre and Vehrencamp, 2008; Searcy *et al.*, 2006). Most threat displays appear to be conventional signaling systems. Examples include color patches and song-type sharing in birds (Molles and Vehrencamp, 2001; Vehrencamp, 2000). Aggressiveness motivation (or willingness to escalate) is most likely to be encoded this way (Hurd and Enquist, 2005).

E. Evolutionary issues

Empirical analysis of aggressive signaling is more complex than the classic ESS modeling approach would suggest. This is in large part attributable to the fact that evolution is not necessarily equilibrial (Houston and McNamara, 1999). An individual's success or failure in using signals depends upon how other individuals use and interpret those signals, that is, it is a trait under frequency-dependent selection (Maynard Smith, 1982). In addition to frequency dependence of the signal phenotype itself, selection pressures acting on signaler and receiver in a communicating dyad may be distinct if their genetic interests or risk profiles (Searcy and Nowicki, 2006) are not identical, or if signals have dual functions, affecting both aggression and mate choice (Wong and Candolin, 2005). Selection may also modify the responsiveness of other individuals to the signals (Arak and Enquist, 1995). Thus, like other significant evolutionary problems such as sexual selection and conflict, signaling strategies may lack stable equilibria and remain in constant evolutionary flux. Understanding the evolution of behavioral phenotypes under such nonequilibrial conditions requires dynamic approaches which have yet to be adequately deployed in the game-theoretical modeling of biological signaling (Hurd and Enquist, 2005).

F. The challenge of "incomplete honesty"

In animal contests, selection should favor displays providing reliable information about the fighting ability or aggressive intent of competitors. However, considerable theoretical work predicts that low levels of deception may occur within otherwise honest signaling systems (Adams and Mesterton-Gibbons, 1995; Számadó 2000). Strategic signals (i.e., ones of intent) are particularly prone to such corruption because they typically involve low production costs (Maynard Smith, 1974, 1979, 1982). Testing for such incomplete honesty is challenging because it is difficult to distinguish dishonest signals from natural variation in signal size (Moore *et al.*, 2009), and between a successful bluff and an honest signal, especially when signaled information is continuous rather than discrete. Hughes (2000) suggested that dishonesty could be detected by analysis of signal residuals, the residuals from a measure of the regression of signal structure on competitive ability. Whereas receivers take advantage of the strong relationship between signal and fighting ability, for example, signalers take advantage of the variation around this relationship. If individuals who exaggerate signals benefit from doing so, they should perform more repetitions of the signaling activity than those who do not exaggerate (Hughes, 2000). Empirical examples of incomplete honesty, though still comparatively rare, suggest this is not a fixed behavioral trait, and depends on context as well as signal residuals (Arnott and Elwood, 2010; Hughes, 2000; Lailvaux *et al.*, 2009).

G. Case studies in aggressive signaling

Using animal models and invasive techniques (e.g., drugs, hormones, brain lesions, and gene knockouts), we have made great strides in unraveling the mechanisms and internal states underlying aggression in controlled lab situations. This is true also with respect to aggressive signaling (see Chapter 5). Studies of nonmodel organisms are a necessary complement to this approach as these can provide the telling exceptions in field situations where more complex social/physical environments permit full expression of behaviors and analysis of adaptive function (see Logue *et al.*, 2010). Below, we present two case studies of taxa employing multimodal signaling systems to artfully modulate aggressive interactions in complex social systems.

II. BIRD SONG SIGNALS AGGRESSIVE INTENTIONS: SPEAK SOFTLY AND CARRY A BIG STICK

The use of song by songbirds provides an excellent illustration of how signals function in aggression in nonhuman animals. The songbirds (suborder Passeres) consist of over 4000 species of birds, which are distinguished in part by their intricate vocal musculature. This musculature functions most importantly in the production of the complex vocalizations from which the songbirds derive their name. Most species in the group are territorial and monogamous, and their songs are used in both territory defense and mate attraction (Catchpole and Slater, 2008; Searcy and Andersson, 1986). At least in temperate zone species, songs are given mainly by males and mainly during the breeding season. Some attributes of song and singing behavior have evolved to function in attracting females and persuading them to mate, but others have evolved to function in aggressive communication between males in the context of claiming and defending a territory.

Many of the signals employed by songbirds in aggressive communication can be illustrated using the signaling behavior of song sparrows (*Melospiza melodia*). Song sparrow songs (Fig. 3.1) are multiparted—that is, they contain multiple phrases differing in structure (Mulligan, 1963). Individual males sing several versions of the species' song, each consisting of a distinct and largely nonoverlapping set of phrases. These distinct versions are called *song types* (Fig. 3.1), and the collection of song types sung by one male is his *song repertoire*. Repertoire sizes vary geographically in song sparrows, with averages in the range of 8–12 song types per male (Peters *et al.*, 2000). Male song sparrows produce their repertoires with "eventual variety," meaning that they sing several to many repetitions of one song type before switching to another. The successive repetitions of a song type are themselves typically not identical, but instead show differences that are audible (Borror, 1965; Saunders, 1924) but of lower magnitude than differences between song types (Nowicki *et al.*, 1994). The minor variations of a song type are termed *song variants* (Fig. 3.1). Song sparrows respond to differences between song variants (Stoddard *et al.*, 1988) but less strongly than to differences between song types (Searcy *et al.*, 1995).

In some species of songbirds, different song types have different functions; for example, in wood warblers (Parulidae) some song types may be specialized for male–female communication and others for male–male signaling (Byers, 1996; Spector, 1992; Weary *et al.*, 1994; but see Beebee, 2004). In song sparrows, however, all song types are thought to be functionally equivalent, and in that sense "redundant." Even with redundant song types, however, certain signals can be produced with a repertoire of song types that are not possible with a single type. Some of these signals have been suggested to be aggressive.

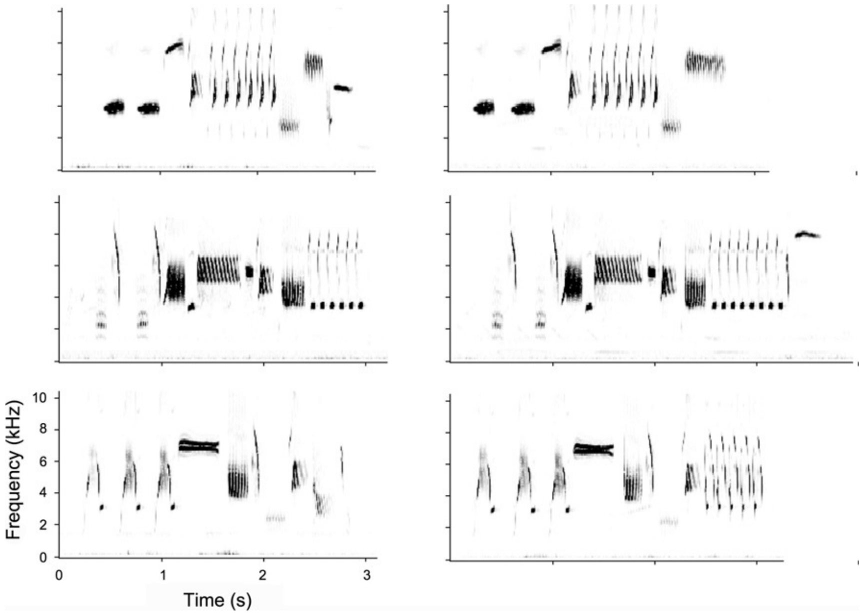

Figure 3.1. Spectrograms of two variants of each of three song types from a male song sparrow recorded in northwestern Pennsylvania. Each row shows two variants of one song type. Note that virtually every note differs between the different song types, whereas the two variants of any one song type tend to differ only in their endings.

Singing behaviors associated with aggressive contexts in song sparrows include:

1. Song-type switching. If a bird sings more than one song type, it can vary the frequency with which it switches between song types, and switching frequency becomes a possible signal. Song-type switching frequency has been suggested to be a conventional signal of aggression (Vehrencamp, 2000)—conventional in the sense that the meaning of the signal is arbitrary with respect to its form. In song sparrows, type-switching frequency increases in aggressive contexts, for example, during counter singing between territorial males or when an outside male intrudes on a territory (Kramer and Lemon, 1983; Kramer *et al.*, 1985; Searcy *et al.*, 2000). In other species, the opposite pattern holds—type-switching frequency decreases in aggressive contexts (Molles and Vehrencamp, 1999; Searcy and Yasukawa, 1990). The fact that either pattern can occur supports the arbitrariness of the signal (Vehrencamp, 2000).
2. Variant switching. In song sparrows, variant-switching frequency also increases in aggressive contexts, and the increase is if anything more consistent than the increase in type switching (Searcy *et al.*, 2000). Given

the evidence that male song sparrows attend to variant switching (Searcy *et al.*, 1995; Stoddard *et al.*, 1988), variant-switching frequency is another potential aggressive signal.

3. Song-type matching. Matching is a behavior in which one male replies to a rival with the same song type that the rival has just sung. Matching can occur by chance, but in song sparrows it has been shown that when wholly or partially shared songs are played to males on or near their territories, those males match the playback songs at levels significantly higher than chance (Anderson *et al.*, 2005; Burt *et al.*, 2002; Stoddard *et al.*, 1992). Song sparrows match strangers more than neighbors (Stoddard *et al.*, 1992), and are more aggressive in general toward strangers (Stoddard *et al.*, 1990), providing further support for matching as an aggressive signal.
4. Song rate. The number of songs produced per unit time is a parameter that birds can vary even if they sing only a single song type. In some species of songbirds, territory owners consistently increase song rates in aggressive contexts (Vehrencamp, 2000). Song sparrows have shown this pattern in some experiments (Kramer *et al.*, 1985) but not in others (Peters *et al.*, 1980; Searcy *et al.*, 2000).
5. Soft song. In her classic monograph on song sparrow behavior, Nice (1943) noted that during intense aggressive encounters, male song sparrows produce songs of especially low amplitude. In some other songbirds, such *soft songs* are produced during courtship as well as during aggression (Dabelsteen *et al.*, 1998), but in song sparrows they apparently are given only in aggressive contexts. Anderson *et al.* (2008) found that the amplitude of soft songs was as much as 36 dB lower than the amplitude of the loudest normal or "broadcast" songs.

The five singing behaviors listed above are all associated with aggressive contexts in song sparrows, but signals used in aggressive contexts can convey submission or escape as well as attack, in which case they would be considered "agonistic" but not "aggressive." These alternative interpretations seem particularly likely *a priori* in the case of soft songs. To test whether a signal is aggressive rather than submissive, it is necessary to determine whether the signal predicts aggressive escalation (Searcy and Beecher, 2009). Aggressive escalation includes outright physical attack of course, but also includes other behaviors that lead up to attack, such as approach to a rival or giving signals that are higher in a hierarchy of aggressive signaling.

A test of the predictive power of singing behaviors was carried out for song sparrows by Searcy *et al.* (2006). In this study, a brief playback of song sparrow song was used to elicit aggressive signaling from a territory owner. After a 5-min period during which displays were recorded, a taxidermic mount of a song sparrow was revealed on the subject's territory, posed above the loudspeaker, in conjunction with another brief playback. The subject was then given a set period of time (14 min) to attack or not attack the mount. Of 95 males that were tested, 20 attacked and 75 did not. The display behavior of attackers and nonattackers was then compared, focusing on the five singing behaviors discussed above, plus *wing-waving*, a display in which a male fans one or both wings while remaining perched; this is the most prominent visual display given by song sparrows during aggressive contests. For the initial recording period, none of the display measures differed significantly between attackers and nonattackers, though the number of soft songs approached significance. A second analysis focused on the 1-min period directly before attack in the attacking subjects, using a matching time period in nonattackers as the control. Here, number of soft songs was significantly higher in attackers than nonattackers, whereas none of the other five measures differed (Fig. 3.2). In single-variable discriminant function analyses, the number of soft songs was the only display that discriminated between attackers and nonattackers; this display correctly predicted presence/absence of attack in 74% of the tested males. Soft song is thus a reliable signal of aggressive intentions in song sparrows.

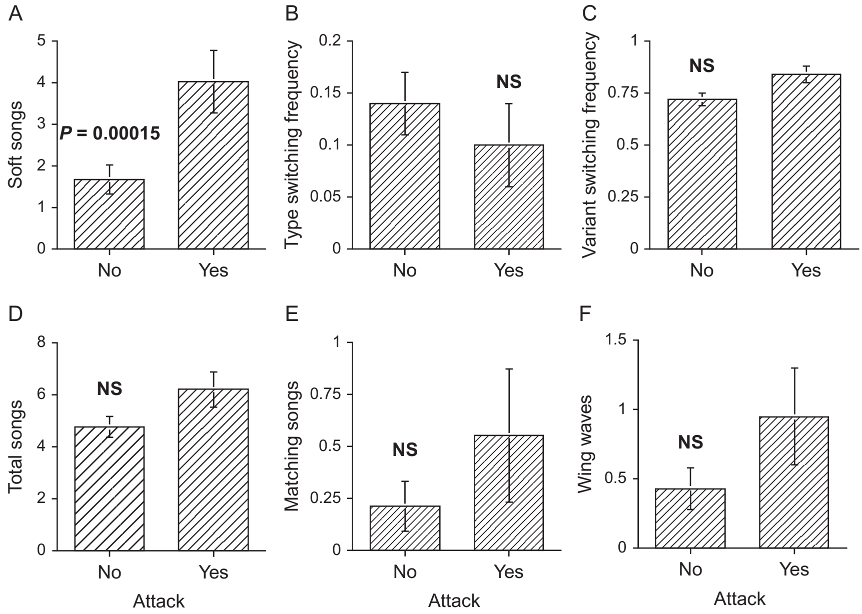

Figure 3.2. Display measures (mean ± s.e.) for the 1 min just prior to attack for male song sparrows that attacked compared to a matching 1-min period for nonattackers. The display measures are (A) number of soft songs, (B) type-switching frequency, (C) variant-switching frequency, (D) total songs, (E) number of matching songs, and (F) number of bouts of wing-waving. Only soft songs showed a significant difference between attackers and nonattackers. Redrawn from data in Searcy *et al.* (2006).

The use of soft, low-amplitude vocalizations as the most threatening of signals is somewhat counterintuitive, but this result has since been replicated in additional species. Ballentine *et al.* (2008) did a parallel study of aggressive signaling in swamp sparrows (*Melospiza georgiana*), a close relative of song sparrows, using methods similar to those of Searcy *et al.* (2006). Swamp sparrows have simpler songs than song sparrows, but again have repertoires of apparently redundant song types. In addition to songs, males give two types of calls in aggressive contexts, *buzzes* and *wheezes* (Ballentine *et al.*, 2008; Mowbray, 1997). In swamp sparrows as in song sparrows, wing-waving is the most prominent visual display given during aggressive encounters.

In 40 trials with swamp sparrows, 9 males attacked a taxidermic mount of a conspecific male and 31 did not. For the initial recording period, five of seven display measures did not differ between attackers and nonattackers; these were switching frequency, number of matching songs, number of broadcast songs, number of rasps, and number of wheezes. Two measures were significantly higher in attackers: number of soft songs and number of wing waves. In a forward, stepwise discriminant function analysis, soft songs entered first, followed by rasps, and these together correctly classified 83% of males as attackers or nonattackers. For the 1 min prior to attack, soft songs and wing waves were again the only two display measures that differed between attackers and nonattackers. For this time period, a discriminant function including soft songs and wing waves was the best predictor of attack, classifying 85% of males correctly.

Hof and Hazlett (2010) have recently performed a similar experiment with black-throated blue warblers (*Dendroica caerulescens*), which are also in the songbird suborder but in another family (Parulidae). In 54 trials with black-throated blue warblers, 19 males attacked the mount and 35 did not. Hof and Hazlett (2010) compared attackers and nonattackers for four display measures: type-switching frequency, total number of songs, number of soft songs, and number of ctuk calls. For both an initial recording period and the 1 min prior to attack, only the number of soft songs differed significantly between attackers and nonattackers, with attackers giving substantially more. In logistic regressions based on either time period, soft song was the only significant predictor of attack. In a logistic regression that incorporated displays for the entire trial, soft song correctly predicted attack behavior in a very impressive 93% of subjects.

In all three of the songbird species reviewed above, most of the displays given in aggressive contexts are not predictive of attack. One theory about such displays is that they were at one time predictors of attack, but that over evolutionary time their reliability was undermined by the spread of bluffing (Andersson, 1980). If an aggressive display is beneficial in intimidating opponents, such that the benefit of giving it is greater than any costs, then selection will favor its use in individuals that do not intend to attack as well as in those that do. Use of the display will then increase in frequency among individuals not intending attack, until at some point the signal ceases to be informative about attack likelihood. Another hypothesis is that these agonistic displays have evolved to convey messages other than imminent attack. Possible alternative messages include at one extreme retreat or submission, but another possibility is for a display to threaten a degree of aggressive escalation that falls short of attack. Song-type matching in song sparrows, for example, has been suggested to be part of a hierarchy of progressively more aggressive signals, which starts with singing a shared song, precedes to type matching, then to staying on the match, soft song, and finally attack (Beecher and Campbell, 2005; Searcy and Beecher, 2009). Because matching is low in this hierarchy of escalation, with several steps intervening between it and attack, matching would not be expected to be very informative about attack likelihood; nevertheless, it might still be predictive of the next level of escalation. Whether matching is predictive in this manner requires further testing.

Among the small number of songbird species that have been studied in this regard, soft song has emerged as an unusually reliable predictor of attack. Why a display whose distinguishing characteristic is low amplitude should be consistently favored for the highest level of aggressive signaling is not well understood. One hypothesis is that by using soft song during an encounter with an intruder, a territory owner lowers the chance of interference from other rival males by preventing them from eavesdropping on the interaction (McGregor and Dabelsteen, 1996), thereby concealing from them that an intrusion is taking place. In contradiction to this idea, Searcy and Nowicki (2006) found that, in song sparrows, more intrusions by third party males occurred during simulated interactions between an owner giving soft songs and an intruder giving loud songs than during interactions in which both owner and intruder gave loud songs. In other words, use of soft songs if anything increased interference by other rivals. A second hypothesis is that soft song is favored as an aggressive signal because its low amplitude makes its target unambiguous: only the male that is being confronted can discern the signal, so only he can be the target. Another way of stating this is that soft song is a performance signal subject to an informational constraint (Hurd and Enquist, 2005) that forces it to be honest at least with respect to the identity of its target.

If a display is a reliable signal of aggressive intentions, as is soft song, then theory predicts that it should be effective in changing the behavior of at least some opponents to the signaler's advantage (Enquist, 1985). In other words, a believable threat should intimidate some opponents, presumably the weaker ones, causing them to concede whatever resource is being contested. Effectiveness in this sense has not yet been demonstrated for soft song, in part because arranging tests of the effectiveness of displays in territorial defense is quite difficult (Searcy and Nowicki, 2000). Recent work with corn crakes (*Crex crex*), which are not songbirds and do not sing, shows that low amplitude calls predict attack, and suggests that these soft calls cause some receivers to retreat (Rek and Osiejuk, 2011). Effectiveness in intimidating opponents has been demonstrated in some other aggressive signaling systems (Dingle, 1969; Fugle *et al.*, 1984; Wagner, 1992).

III. VISUAL DISPLAYS SIGNAL AGGRESSIVE INTENT IN CEPHALOPODS: THE SWEET SMELL OF SUCCESS

Cephalopods—squid, octopus, and cuttlefish—are marine molluscs with large complex brains and highly diverse behavior (Hanlon and Messenger, 1996). They are highly visual animals, exemplified partly by their huge optic lobes that represent more than half of their central nervous system. These soft-bodied cephalopods are renowned for their rapid adaptive coloration: individuals of each species can instantly (<1 s) switch between any of 10–50 body patterns that are used for a wide range of communication and camouflage. The appearance of the animal can change so dramatically that they sometimes appear to be different species. This capability has been termed rapid adaptive polyphenism because the same genotype can produce multiple phenotypes.

Squids and cuttlefish have complex mating systems and their sexual selection mechanisms have been studied in some detail. During spawning, the operational sex ratio ranges from 2–4 M:F in some species to 4–11 M:F in others (e.g., Hall and Hanlon, 2002; Hanlon *et al.*, 1999, 2002; Jantzen and Havenhand, 2003). Thus, competition among males for mates is often intense and the visual signaling involved with male rivalry is diverse and dramatic in some cases. These agonistic visual displays are highly developed, and a few experimental studies have complemented field studies to determine the nature of aggression.

One of the most interesting aspects of agonistic behavior in cephalopods is its facultative nature. That is, small unpaired males seek extra-pair copulations using various "sneaking" tactics, but these are usually nonaggressive tactics that actively avoid confrontations with the paired males (for an unusual case involving sexual mimicry, see Hanlon *et al.*, 2005). However, if the large consort male leaves or is displaced (experimentally—in the field or lab), the small males immediately recognize the new behavioral context and become paired consorts to the female and will use agonistic displays to ward off other small males. This transition between sneaker/nonaggressive and consort/highly aggressive is quite remarkable for its speed and fluidity, and testifies to the cognitive abilities of these marine invertebrates. Many fishes and invertebrates have obligatory (i.e., genetic) sneaker morphs (Gross, 1996), but cephalopods accomplish this facultative switch with a large brain and extensive nervous system.

Early game theory models of agonistic behavior predicted that animals should not signal their probability of attack to their opponents. As Maynard Smith (1982) argued, if animals signaled their aggressive motivation during a fight, there would be strong selective pressure for animals to "bluff" and to signal the highest motivational state possible; such a system would likely be invaded by cheaters and become unreliable. However, some animals do signal intent (Hauser and Nelson, 1991), and below we provide an unusual example of this in cuttlefish.

As in birds, cephalopods signal aggressive intent but they do so with visual signals (chromatic skin patterns) as well as body postures (parallel positioning and arm postures). Two examples are given: one from cuttlefish (Order Sepioidea) and one from squid (Order Teuthoidea). In addition, a new finding is described in which a molecular trigger of aggression has been found in squid.

A. Cuttlefish agonistic bouts

In the Intense Zebra Display of the European cuttlefish, *Sepia officinalis*, the males turn on high-contrast stripes and dark eye ring and extend their large 4th arm toward the opponent (Fig. 3.3C). Such agonistic encounters between males can lead to aggressive grappling and biting. The experiments of Adamo and Hanlon (1996) showed that one visual component of the display—the *facial darkness*—was by far the most highly variable in expression, and was a good predictor of outcome in encounters in which one male withdrew. In non-escalated encounters, the male that ultimately withdrew always maintained a less dark face than its opponent (Fig. 3.3A). When the face of a displaying cuttlefish became lighter, the other male either remained in the Intense Zebra Display but did not approach closely or lightened the intensity of its own display within 15 s. When both males maintained a dark face, the agonistic encounters usually escalated to physical pushing, and sometimes to grappling and biting (Fig. 3.3B).

Why would males show an agonistic display to a rival male but simultaneously signal their intent not to be aggressive? Adamo and Hanlon (1996) pointed out that sexual recognition in cephalopods is poorly developed, and that the Intense Zebra Display (with 4th arm extended) identifies the signaler as a male. The authors suggest that male cuttlefish that are not prepared to attack an opponent still give the modified (i.e., light-faced) Intense Zebra Display to convey two messages: (1) that it is male, but (2) it is not prepared to escalate to aggressive physical contact. As the authors point out, when agonistic displays perform more than one function, signaling intent (i.e., signaling its likely subsequent behavior) can be an ESS. Unless the fight escalated to grappling and biting, there would be little cost to cheaters in this system since males that

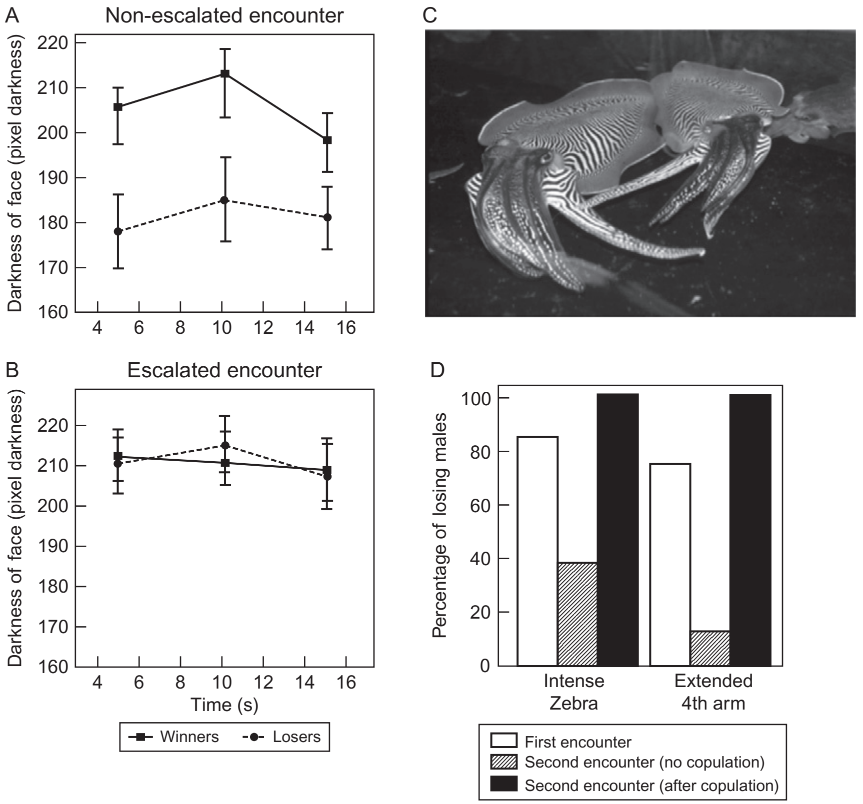

Figure 3.3. Cuttlefish signal intent to escalate a fight with a *dark face* component to their Intense Zebra Display. (A, B) Differences in facial darkness during a non-escalated versus escalated encounter. (C) Two males in Intense Zebra Display with different degrees of *facial darkness*. (D) When males that lost a fight copulated with a female, they became more aggressive in the successive fight. From Adamo and Hanlon (1996).

bluffed (i.e., gave a dark-faced Intense Zebra Display but had little fighting motivation and/or ability) could withdraw at the next stage of agonistic behavior with little penalty.

In the same study, the authors allowed losing males to copulate with a female after a bout, and retested them with the male each had lost to. The former losers increased facial darkness dramatically in those encounters, showed a long-lasting Intense Zebra Display, and did not withdraw from an opponent (Fig. 3.3D), thus supporting the contention that facial darkness signals the animal's motivational state (i.e., tendency to attack).

B. Squid agonistic bouts

Male–male fights in *Loligo plei* are complex visual displays that include up to 21 behaviors. There is a hierarchy of agonistic signals that sometimes culminates in an aggressive physical lateral display and fin beating (Fig. 3.4A and B), which are then followed by *chase* or *flee*. DiMarco and Hanlon (1997) tested whether dominance was based upon the duration or frequency of these behaviors, but it was not. Instead, they found that certain visual features such as the *lateral flame markings* (Fig. 3.4B, top squid) could be expressed with high contrast and that this was a visual factor in escalation of the agonistic bout.

Two distinct tactics were exhibited by fighting males in this set of laboratory experiments: (1) long bouts with slow escalation from visual signaling to chasing and fleeing, or (2) short bouts with very rapid escalation from visual signaling to lateral displaying, aggressive physical fin beating, followed by chasing and fleeing (Fig. 3.4C). It is noteworthy that the second tactic occurred when a female was present (i.e., when a potential *resource value* was present). As shown in Fig. 3.4D, the presence of a female in various combinations had a dramatic effect on the nature and duration of the agonistic interactions. Longest bouts (mean 14 min) occurred when only two males were present. Bouts became progressively shorter when either two males and one female were assembled simultaneously, or two males were interacting and a female was then added (mean 9 and 3 min, respectively). But when a male and female were put in a tank and allowed to pair, and then a nonpaired male was added, tactic 2 was used and the highly aggressive interaction lasted only 30 s (a 28× difference over the simple two male scenario). As a control, when females were added to male/female pairs, there were no agonistic interactions (Fig. 3.4D).

In this squid species, the lateral display represents an escalation of aggression because it involves parallel posturing and the simultaneous expression of many high-contrast visual signals, which collectively give the impression of making the squid look larger (e.g., the mid-ventral ridge of the mantle protrudes vertically as in the dewlap extension of geckos). Fin beating is a physical, robust contest of pushing that can transmit information about strength and size of the competing individuals.

C. From molecules to aggression: Contact pheromone triggers strong aggression in squid

In the squid *Loligo pealei*, which conducts visual agonistic bouts similar to L. plei (above), it was found recently that females deposit a contact pheromone in the outer tunic of egg capsules that they lay on the sea floor. When males see the egg capsules (even in the absence of females), they are visually attracted to them and then physically contact the eggs, which leads to extremely aggressive fighting

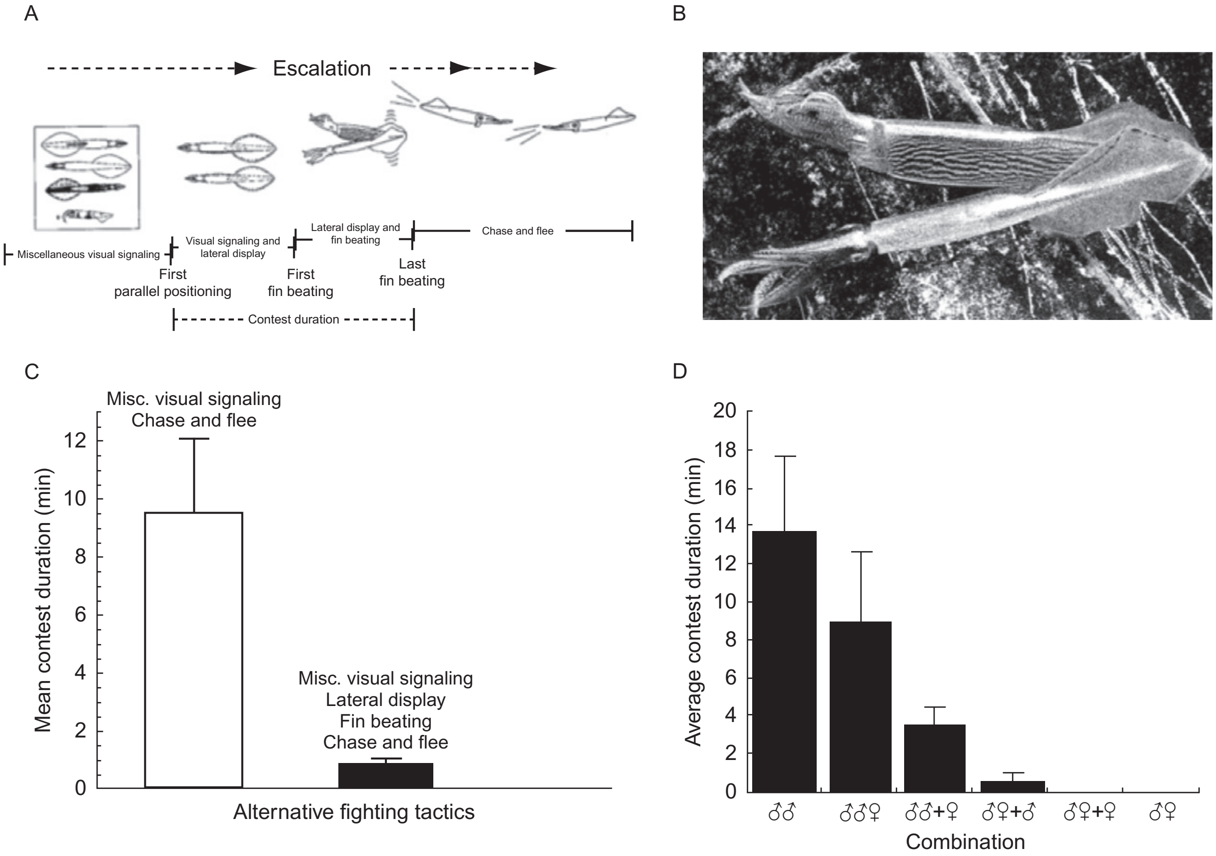

Figure 3.4. Male squid (*Loligo plei*) use complex lateral displays to conduct shorter fights with higher aggression when a resource value (i.e., a female mate) is present. (A) Schema depicting the escalation pathway to a typical fully escalated agonistic contest. (B) Photograph of a fully deployed lateral display and fin beating. The display comprises six visual components: arm spots, dorsal arm iridophores, stitchwork fins, mid-ventral ridge, tentacular stripe, and lateral flame. (C) Short fights are more complex and involve lateral displays and physical fin beating. (D) The shortest, most dramatic fights occur when a mating pair is already formed, and a rival male is introduced to the tank (♂♀+♂).

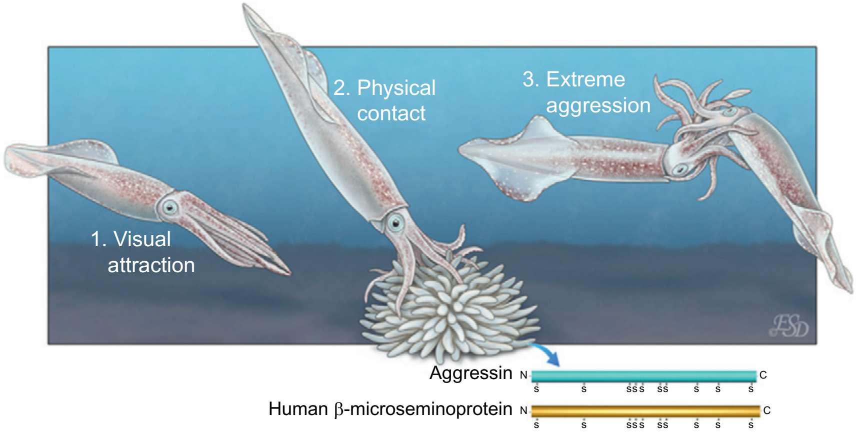

Figure 3.5. When male squids see egg capsules on the sea floor, then approach and touch them, this leads to immediate and dramatic change from calm swimming to extreme fighting. The contact pheromone ("aggressin" or *Loligo* β-MSP) is in the tunic of the egg capsules and is similar in structure to that found in humans, mice, and other vertebrates.

within a minute or two (Fig. 3.5) (Cummins *et al.*, 2011). Thus, there is a two-step sensory process: visual attraction to eggs followed by contact chemoreception that induces onset of aggression.

In controlled experiments, the 10 kDa protein pheromone (termed *Loligo* β-microseminoprotein, β-MSP) was isolated and coated onto a clear glass flask containing egg capsules, and males that touched the glass (but not the eggs) began to signal, fight, and bite each other violently within seconds. Glass flasks without the pheromone coating failed to elicit those aggressive behaviors. Thus, direct contact with the protein molecules immediately led to the full cascade of complex aggressive fighting in the absence of females. Given that aggression is often considered to be a result of multiple interactions of physiology, hormones, sensory stimuli, etc., this finding reminds us that perhaps in some cases there are straightforward pathways to aggression. In fact, the proximate mechanisms that trigger or strengthen aggression are not well known for many taxa (Wingfield *et al.*, 2005).

There is a noteworthy vertebrate/mammalian connection to this finding. As shown in Fig. 3.6, the β-MSPs are highly conserved throughout the animal kingdom. The greatest known concentration of β-MSPs is in human and rodent seminal fluid, yet regrettably the functions of β-MSPs are unknown in any taxa except cephalopods, as explained above (Cummins *et al.*, 2011). As those authors suggest, it would be worthwhile to look for an aggression function for

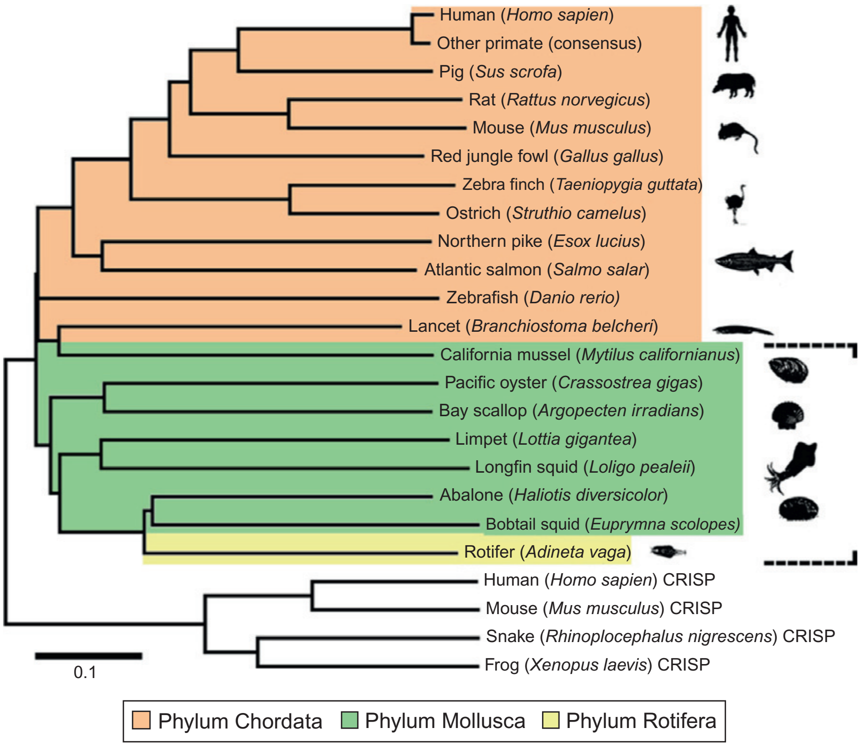

Figure 3.6. Evolutionary origins and conservation of β-microseminoproteins. The tree shows phylogenetic relationships among the protein sequences. The β-MSPs identified in the Cummins *et al.* (2011) study are within the dotted lines.

β-MSPs in mammals and other vertebrates, given the molecular similarity and unique structure of these proteins, all of which seem to be most concentrated in exocrine glands in many taxa. Such findings remind us that multisensory cues are often involved in stimulating behaviors and that a good deal more research is needed before we understand subjects such as aggression.

D. Signaling aggression in humans

In humans, as in other species, signaler and receiver have both evolved to use variation in aggressive signal structure to their own advantage. In the case of human speech, fundamental vocal frequency is perceived to be associated with social cues for dominance and submissiveness (Bolinger, 1978; Huron *et al.*, 2009; Ohala, 1994), with vocal pitch height used to signal aggression (low pitch), or appeasement (high pitch). Moreover, a strong correlation with eyebrow position suggests an intermodal linkage between vocal and facial expressions (Huron *et al.*, 2009). Evidence implicates male dominance competition (Puts *et al.*, 2006), rather than intersexual selection (see Chapter 2), as the selective origin of this performance signal. Similarly, handgrip strength is correlated with level of aggression and appears to be an honest signal for quality in males (Gallup *et al.*, 2007). Mathematical models show, however, that the tradeoff of deceptive efficacy and dishonest signals of intent often favors signalers who produce imperfectly deceptive signals over perfectly honest or perfectly deceptive ones (Andrews, 2002). Competition among coalition groups (a characteristic shared with chimpanzees) initiated a social arms race, culminating in extraordinary human cognitive abilities (Flinn *et al.*, 2005), capable of parsing aggressive signals (Paul and Thelen, 1983), and competitive displays (Hawkes and Bird, 2002). This great capacity for signaling is outstripped only by the uniquely human ability to extend our phenotype with weaponry—with the unfortunate consequence that our potential to inflict damage frequently exceeds our ability to control aggression.

Rather than maximizing its absolute amount, natural selection enhances the overall *effectiveness* of aggression. In invertebrates, where individuals generally pursue a solitary existence, physical superiority primarily determines the eventual outcome of contests, and most fights are quickly resolved on the basis of prominent asymmetries in body or weapon size. In vertebrates, which must navigate the demands and opportunities of social living, aggressive success is largely contingent on the development of social competence. In this case, natural selection favors those with an ability to effectively anticipate their chances well in advance of a contest, and to signal strength while hiding any intentions to eventually withdraw. Generating and interpreting aggressive signals to form successful alliances and to inherit status from high-ranking kin, is thus key to winning both short-term contests and long-term evolutionary success.

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