

## Chapter 8: The Games Animals Play

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## Conflicts and Evolutionary Game Theory

The notion of a game seems to conjure up a vision of light-hearted contestants engaged in the pleasant pursuit of recreation. While some human games have this quality, animal contests do not. Often, combatants inflict severe injury. Certainly in contests between countries, war is a less desirable form of “conflict resolution”, compared to the more peaceful solution of diplomacy. Are there analogies that can be drawn between human gaming, conflict, and conflict resolution that we can apply to animal behavior?

A game can be defined as a means of reaching a decision in a conflict situation in which one contestant wins at the expense of another. Von Neumann and Morgenstern (1953) developed game theory to explain human behavior in conflict situations. The Nobel Laureate James Nash developed the key concept of a **Nash equilibrium**, which is the stance a rationale player should take in contests. Maynard Smith and Price (1973) came up with a similar concept, which we call the **ESS** or *Evolutionarily Stable Strategy*. Like optimal foraging theory, which was discussed in previous Chapters 6-7, game theory was developed as a way to explain costs and benefits that arise from economic decisions. Evolutionary game theory differs from optimal foraging theory in that attempts are made to address long-term evolutionary contests between individuals of a species. Optimal foraging theory is usually applied to energy maximization. The currency in game theory is typically fitness, while the currency in optimal foraging is energy. The application of game theory to the evolution of behavior has been very successful compared to applications in economics because **payoffs** from a game of life are measured in terms of fitness (i.e. survival, reproductive success), whereas payoffs in economic games or social conflicts are measured in a more abstract quantity called expected utility (Maynard Smith 1982).

When animals compete for a resource conflicts inevitably arise. Much of the discussion of optimal foraging assumed that animals rarely interact, and when territoriality was considered, conflict resolution was not considered. How do animals resolve these conflicts? What are the costs of conflict and when is it necessary to escalate the contest to stages in which injury is more likely? What is the value of restraint?

## The Hawk-Dove Game and The Evolution of Lethal Fighting

The Hawk-Dove game was designed to explore a widespread phenomenon in animal conflicts: although contests are frequently vigorous, lethal fighting is rare. If lethal fighting is rare, what is the evolutionary value of restraint (Maynard Smith and Price 1973)? Assume two animals meet and contest a resource. The two contestants have different behaviors. Hawk fights at the drop of a hat. Hawk always fights, even against other hawks. When injured hawk retreats (or dies). Dove backs down as soon as the contest escalates to a fight and is never injured. The hawk-dove game explores the evolution of restraint by addressing the limits on lethal fighting. Who will win?

The theory for the hawk-dove game (Side Box 7.1) shows that hawk is an **Evolutionarily Stable Strategy** which is the unbeatable strategy in the long run: hawk can invade when it arises as a rare mutant, but once Hawk increases to high frequency, hawk is not invadable by the other defined strategy called Dove. Dove cannot invade hawk, yet hawk can always invade dove.

In this game with two kinds of chess pieces it seems that life is quite boring. One piece always loses to the other. With the rules described above, if you were to choose to play the game in a single guise, you would choose Hawk. Nobody would want to play the dove, because nobody wants to be a loser.

However, if the cost of fighting is too high for Hawk, the game gets a little more interesting. Under these conditions, it can be shown that the population exists in a mixture of the two strategies (see Appendix 3). A rare mutant dove can invade because when Hawks are really common they can eliminate each other (probabilistically) during their contests.

Hawk can still invade a population of doves because dove always loses to hawk. If fighting is lethal then the population consists of both Hawks and Doves and a strategy of restraint is possible. On the other hand, when fighting is not lethal, the whole population practices restraint in the sense that no one dies, but the population consists entirely of non-lethal fighting hawks. The hawk-dove game, while simple, describes a common pattern in animals -- they rarely kill each other.

### Side Box 7.1. Hawk-Dove Game and Evolutionary Stable Strategies

Two animals meet at a resource. The resource adds a value,  $V$ , to an individual's fitness. Each animal can adopt one of two strategies: 1) hawks behave aggressively until one opponent is injured and the contest is won, or 2) doves display, but retreat if their opponents are aggressive. Strategies have costs and benefits, which yields a net payoff.

When two animals play hawk, the cost of losing is given by the cost,  $C$ , since one of the opponents is going to be injured. Either contestant has a  $1/2$  probability of losing so the average cost is  $C/2$ . Likewise, each hawk gains an average resource value of  $V/2$ . The net payoff for each individual hawk would be  $V/2 - C/2$  or  $(V - C)/2$ . When two animals play dove, there is no cost to the doves. Each dove has a  $1/2$  probability of winning so they divide the resource and the net payoff is  $V/2$ . When a hawk meets a dove, the hawk always wins at no cost, so the net payoff for the hawk is  $V$ . Conversely, the dove that engages the hawk gains nothing, but experiences no cost so the net payoff is 0. Game theory summarizes the outcome of all possible encounters in terms of a payoff matrix that describes the fitness of each strategy when playing against an opponent.

		Common type	
		Hawk	Dove
Rare type	Hawk	$\frac{V - C}{2}$	$V$
	Dove	0	$\frac{V}{2}$

Which strategy is the winner in the long-term? For a strategy to be an **Evolutionarily Stable Strategy** or an **ESS**, two conditions must be met.

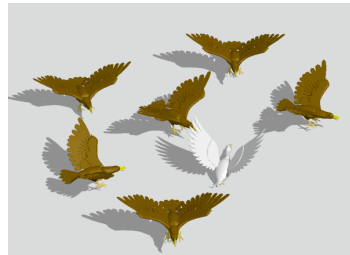
1. When the strategy enters the population as a rare mutant it must be able to invade and spread against other common strategies.
2. Once the strategy becomes common, the ESS is itself uninvadable by all other rare mutant strategies.

Consider a rare mutant hawk that has invaded a population of doves. The hawk obtains fitness,  $V$ , against dove. In contrast, any pair of doves in a population of doves gets fitness,  $V/2$ . The mutant Hawk has higher fitness than individual doves (e.g.,  $V > V/2$ ), and hawk invades dove. Consider a mutant dove that invades a population of hawks. The dove



has a fitness of 0 when playing hawk. In contrast, any pair of hawks in a population of hawks gets an average fitness of  $(V-C)/2$ . Dove cannot invade as long as  $0 < (V-C)/2$ , which yields  $C < V$ . Thus, dove cannot invade if the cost of a fight is less than the value of the resource. When fighting is not lethal, hawk is an ESS

that can invade dove when rare, but is uninvadable by dove when hawk is common. Can dove ever invade? The strategy dove can invade if  $0 > (V-C)/2$ . Solving  $0 > (V-C)/2$  we obtain the conditions for dove to invade. If  $C > V$  dove can invade, or if the costs are greater than the value of the resource, doves can invade. This would imply that when fighting is lethal among hawks, dove can invade. Hawks kill each other off, and doves can clean up the “spoils” of the isolated wars between hawks. When costs exceed the value of the resource ( $C > V$ ), every fight will leave one hawk in a weakened position.



A more complicated derivation (given in Appendix 3) shows that if  $C > V$ , the frequency of hawks ( $p$ ) and doves ( $1-p$ ) in the population will be determined by  $p=V/C$ . There are two genetic solutions to this equilibrium frequency: the population is composed of hawks with frequency  $p$  and doves with frequency  $1-p$  or all individuals play hawk and dove, but their strategy should be to play each with a probability  $p$  and  $1-p$  respectively.

The metaphor of hawks and doves becomes strained if taken too literally. In fact the terms Hawk and Dove do not refer to any animal, Maynard Smith and Parker (1976) coined the terms from a dichotomous 1970's political ideology used to categorize Hawks, who were for the war in Vietnam *versus* Doves, who were against the war. Many ESS models are not meant to accurately capture all aspects of biology; rather, they are meant to capture the essence of the game that might underlie

interactions between individuals in a species. Thus, in a population of aggressive (e.g., metaphorical hawks) and timid individuals (e.g., metaphorical doves), the aggressive individuals will have an advantage provided the costs of the contest do not exceed the value of the resource.

Beyond this abstraction, there are some simple natural situations where the theory has applicability (Reichert 1982; Reichert 1984). Funnel-web building spiders, *Agelenopsis aperta*, are commonly found in grassland habitats throughout North America. Territorial spiders defend the location in which they build their web against floaters that roam the habitat in search of a web that they can take over. In contests between two spiders that have a large asymmetry in body size, the spider with the largest body size will usually win. The larger spider immediately uses threat displays and attempts to make physical contact, which is potentially dangerous to the smaller combatant. The smaller combatant immediately withdraws. This contest is very much like a hawk-dove contest in that the larger spider has a hawk-like strategy and the smaller spider has a dove-like strategy (Reichert 1984).



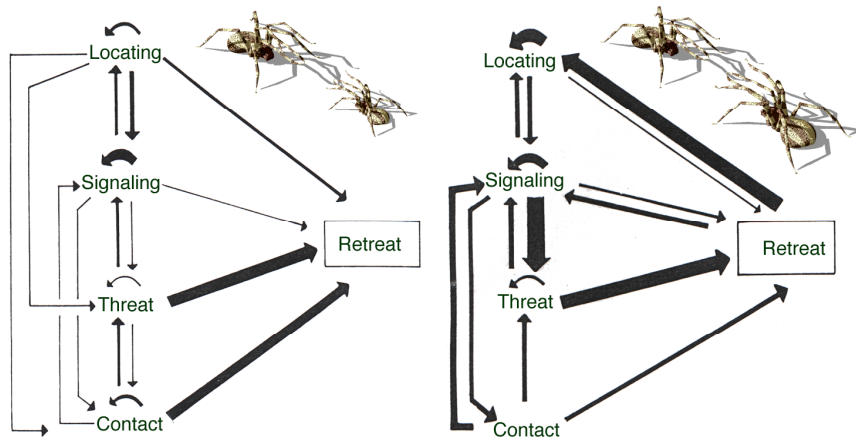
Figure 8.1. *Agelenopsis aperta* spiders that are web owners have contests with both roving spiders (dashed intrusion) and neighboring web-owners (dotted intrusion). Contests between web-owners and rovers are over the control of territory, a valuable resource. Contests between neighbors might be over a prey item, which is a low-value resource. From Reichert 1982).

What about contests involving opponents that are similar in size? In such contests, two spiders do not immediately advance to physical contact and threat. There is usually a slow escalation of the contest through signaling behaviors in which vibratory displays, which involve tapping or plucking of the web strands, or visual displays are used in a very stereotypical fashion. The spiders will often rear-up (perhaps in an attempt to increase apparent size), wave their legs, flex and stilt by moving up and down on all legs. The contest between two combatants involves more ritual than actual fighting. A gradual escalation of the contest has been referred to as a Graduated-Risk contest. As the contest

proceeds, the combatants are more willing to accept the risks associated with escalation.

Figure 8.2 Transitions between behavioral states in funnel web spiders, *Agelenopsis aperta*, that are involved in territorial disputes when combatants are asymmetric and symmetric in body weight. Intensity of interactions is graded from locating, signaling, threat, and contact behaviors that ultimately lead to fighting. Width of arrow depicts frequency of movement between each behavior. Asymmetric contests behave with rules similar to Hawk-Dove and the larger opponent threatens the smaller, which leads to retreat of the smaller. In contrast, symmetrical contests lead to a long series of movements such as locating, signaling, and threatening gestures. They rarely lead to physical contact. Redrawn from Reichert (1982).

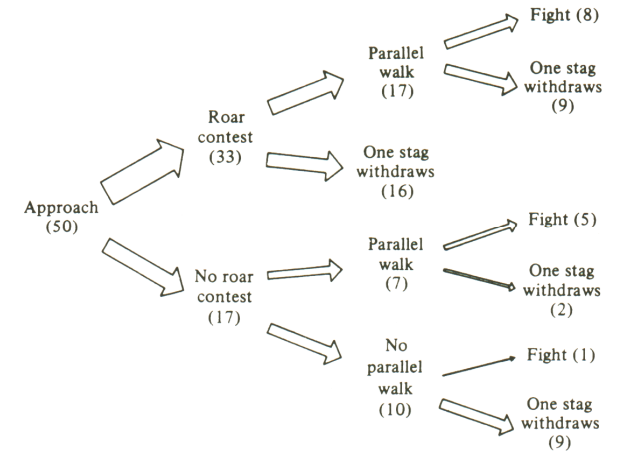
### The Value of Ritualized Fighting



It is often the case that animals, which are evenly matched in fighting ability, will use ritualized displays during the early phases of a contest. For example, male red deer stags, *Cervus elephus*, have a large rack of antlers that could easily deliver a mortal wound to their opponents. Rather than attempt to deliver the fatal blow immediately, the stags will first engage in a roaring contest. If the roar does not intimidate the rival, the stags will then engage in a parallel walk. The kind of information that combatants get from the stereotyped parallel walk is unclear, but the stags may be attempting to size each other up (Clutton-Brock and Albon 1979). Finally, if neither stag backs down, the stags will escalate to a

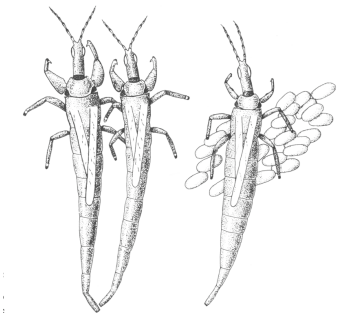
locked-horns contest, which may lead to mortal combat.

Figure 8.3 Transitions between behaviors for two red deer stags, *Cervus elaphus*, that are contesting a harem of females. Only 14 of the 50 contests resulted in a fight and the vast majority of fights, 13, were preceded by a ritualized display (e.g., either a roar or parallel walk). From Clutton-Brock and Albon (1979).



Even the diminutive thrip, a small insect that is the size of a rice grain, will use a parallel bout (Fig. 8.4), which is a display reminiscent of the parallel walk in stags (Crespi 1986). Equally matched opponents are much more likely to use this display to size each other up. However, when the asymmetry in size is great between defender and challenger, the larger individual usually wins the contest (Fig. 8.5).

Figure 8.4 The diminutive thrip engages in a display were males side up beside one another in a 'parallel bout', which appears to be a sizing up display. A female is also shown with eggs (from (Crespi 1986)).



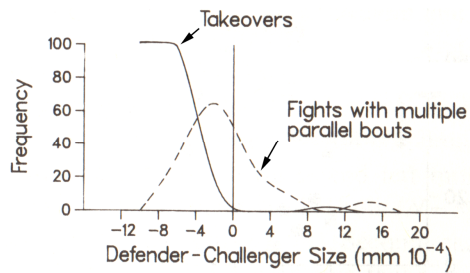


Figure 8.5. Fights between thrips with parallel bouts are far more likely when the defender and challenger are more equal in size. When the defender is smaller than the Challenger, the challenger can easily take over the defender's resource, a female (from (Crespi 1986)).

Why should stags engage in a roar or the parallel walk instead of escalating to an all out fight? Why are thrips so quick to lose when small? Why should spiders and thrips that are symmetrical in body size engage in much more lengthy threat and signaling displays? What is the evolutionary value of such ritualized contests? When is restraint an *Evolutionarily Stable Strategy*?

Consider three strategies: 1) *hawk* that escalates to conflict immediately, 2) *dove* that engages in a ritual display immediately but backs down when attacked, and 3) *retaliator* that initially engages in a ritual display with any opponent (dove or hawk), but when threatened by a hawk it escalates in retaliation against a hawk. Retaliator's strategy drives off doves immediately, but retaliator must escalate to drive off the hawk. An analysis of the payoff matrix for this contest shows that retaliator is an ESS if the costs of fighting is greater than the value of the contest. A rare mutant retaliator invades dove because retaliator can escalate to a hawk-like stance. However, as in the case of the Hawk-Dove game where we saw that lethal fighting leads to a less-than-lethal ESS, the same is true for Hawk-Dove-Retaliator. When fighting is potentially lethal, retaliator is an ESS because it can invade hawk and dove. Moreover, neither hawk nor dove can invade retaliator, when fights are lethal, and thus ritualized contests are favored over contests without ritual. However, the ability to opt for lethal contests is retained as a last-resort behavior to win contests.

When males are equally-matched in size, they are generally slower to escalate to a fight, and a longer fight duration is typically observed in a wide variety of taxa including crayfish (Rubenstein and Hazlett 1974), several crab species (Hazlett 1968; Warner 1970), the Siamese fighting

fish (Figler 1972), and the cichlid fish, *Nannacara anomala* (Enquist et al. 1990). With a lack of a clear discrepancy in size between opponents, males must acquire information regarding their opponents. As they engage in ritualized contests, they are probing their rivals for information regarding their strengths and whether or not they themselves have weaknesses. Obviously, the acquisition of information regarding asymmetries between themselves and their opponents takes a little time.

### The War of Attrition

The variations on the Hawk-Dove game discussed above show that the advantage of fighting behavior can be offset by the cost of lethal fighting. A cost-benefit analysis also shows that when resource value is low compared to the cost of fighting, restraint is adaptive (actually this will be a mixed ESS -See Side Box 8.1, or the retaliator game). The War of Attrition (Maynard Smith, 1973; Maynard Smith, 1974) is another game that makes simple predictions about contestants based on fighting ability. Another name for the war of attrition is "the waiting game" because the winner of the contest is able to persist longer.

The war of attrition is a situation where there are an infinite number of possible strategies (e.g., many possible persistence times for the winner). It is assumed that the cost of persisting increases in a linear fashion with time. When one individual gives up, the other contestant gets all of the resource, and both individuals incur the cost of persistence that have accrued. Obviously, each individual would do better by persisting longer than its opponents, and thus no pure persistence level would be evolutionarily stable. Because no single persistence time is stable, the best strategy is an unpredictable persistence time (Parker and Thompson 1980). This would imply, that individuals will not divulge any information regarding their likelihood of quitting the contest, because any information could be used by the opponent to persist that much longer and win. The war of attrition suggests that symmetrical opponents will withhold all information from their competitor.

Austad (1983) tested the utility of the war of attrition in determining the outcome of male contests in male bowl and doily spiders, *Frontinella pyramitela*. When male web-building spiders mature, they abandon their

webs to search for females. In the previous example, of funnel-web spiders, *Agenopsis aperta*, the contests were over a territory (above). The value of a territory is less intimately related to an organism's fitness compared to the direct benefit of copulation. Accordingly, ritualized contests are quite common in territory defense because the value of the territory does not immediately impact fitness. However, male bowl and doily spiders are fighting over access to females and they are less likely to use ritualized conflict. The fitness return from copulating with a female is immediate, the male spider sires some of her progeny. Because the value of return is high, they might be expected to routinely engage in potentially damaging contests.

A simple prediction from the war of attrition is that contests between symmetric or equally matched opponents should lead to longer battles than asymmetric contests between opponents that are unequally matched. Male bowl and doily spiders do engage in damaging grappling contests. One of the assumptions of the war of attrition model is that contests rise linearly with persistence in the contest. Grappling contests and injuries occurred more rapidly in contests between different-sized combatants than those contests in which combatants were the same size (Fig. 8.6). Contests between combatants that were symmetrical in size lasted much longer than contests with a large asymmetry in size between the male bowl and doily spiders (Fig. 8.7).

Figure 8.6. Costs of grappling contests in male bowl and doily spiders, *Frontinella pyramitela*, as a function of contest length for different-sized combatants. Equal-sized combatants engage in a longer-lasting war of attrition compared to different-sized combatants (from Austad 1983).

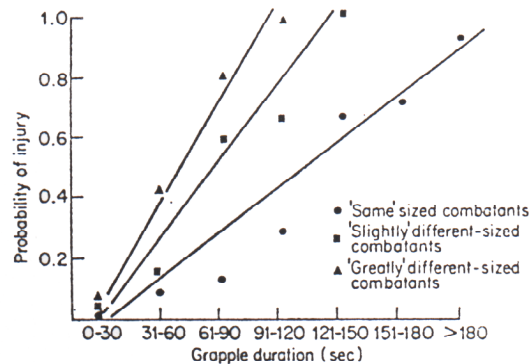
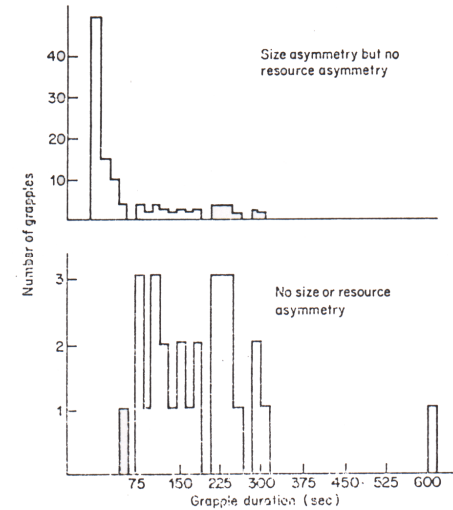


Figure 8.7. Length of grapple contests for male bowl and doily spiders with a size asymmetry and

males that are symmetrical in size (from Austad 1982).



### Knowledge of the Resource and Asymmetry in Motivation

A lot of attention has been directed at the effects of asymmetries on the strategic choices of animals. The war of attrition treats the opponents as symmetric, but variations on the game introduce two kinds of asymmetry into contest behavior (Maynard Smith 1982):

1. The simplest of the asymmetries can be thought of as a **home field advantage**. Invariably, a territory holder has an advantage over intruders.
2. The second kind of asymmetry arises when one contestant has more to gain or lose from the battle and is therefore more motivated to persist during a contest. A classic case involves a territory holder versus an intruder. The territory holder has a lot invested in the territory. The territory holder has knowledge of safe retreats, or knowledge of resources. All of this information makes the territory more valuable to the territory holder than to the intruder.

The home field advantage really refers to an animal's state of mind and it's "psychological" edge in battle. It is possible to perform simple experiments that cause two individuals to perceive that they are the owner of the same territory (Fig. 8.8). Male speckled wood butterflies, *Pararge aegeria*, vie for coveted light gaps in the forest that are used to

display to females. Normally, a resident male will win any contest against a non-territorial male. Removing a current territory holder even for a few seconds allows a non-territorial male to settle on the territory.

Figure 8.8. The home field advantage addressed in experiments on the speckled wood butterfly, *Pararge aegeria*. The resident (white) always wins contests with a non-territorial male (black). However removing the owner allows the non-territorial male to establish a home field advantage within seconds and beat the old resident. From Davies (1978).

The new resident now gains the “home-field advantage”. When the original territory holder is re-released on his territory, the new resident can easily displace the original resident. This is true even if the swap takes place within minutes. There is clearly not enough time for the new resident to gain knowledge

about the territory that might give him an edge. There is no obvious physical advantage because the new resident excluded the old resident in an encounter where the old resident still had the perception of a home field advantage. Thus, the physical presence on the territory is enough to give a new resident an edge or a ‘home field advantage’. It seems then that ownership might have its privileges. In the case of the speckled wood butterfly the value of the resource is a sun patch to attract females. The cost of battle entails serious risk. Damage to the wings may reduce aerodynamic efficiency. Why fight against the owner when another patch is available somewhere in the forest. However, butterflies are easily tricked into contesting the resource if they both think that they are owner. They fight viciously.

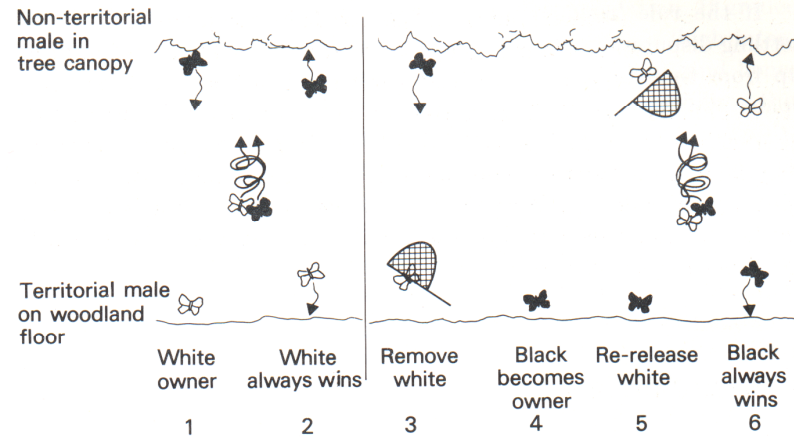
A very simple ESS model that seems to provide a reasonable explanation of home field advantage of butterflies is a modification of the Hawk-Dove game. These strategies are as described above, but with the addition of a bourgeois strategy (Maynard Smith and Parker 1976). Bourgeois behaves like hawk on its home turf, but it behaves like dove

when invading someone else’s turf. The predictions from the game are fairly simple, hawk is always the unbeatable strategy if resource value is greater than the costs of fighting ( $V > C$ , as for the Hawk-Dove game, see Side Box 1.1). However, if value of the resource is less than cost of fighting then bourgeois is the only ESS. This differs from the case of Hawk-Dove in which hawk and dove would be found as mixed strategies in the population according to the ratio  $p = V/C$ .

Male Hamadryas baboons in the deserts of the Middle East appear to show a similar home field advantage with regards to their control of females (Kummer et al. 1974). Male baboons often form long-lasting pair bonds with females in which the male is the only one to engage in copulation with the female. If male baboon ‘A’ is allowed to form a pair bond, and male ‘B’ is allowed to watch the union, ‘B’ will not challenge ‘A’ for ownership. If ‘B’

forms a pair bond with another female, ‘A’ will likewise not challenge ‘B’. However, if ‘A’ and ‘B’ form a pair bond with a female at the same time and the two are not aware of the other’s involvement, then escalated fighting will occur between ‘A’ and ‘B’. When the two baboons realize they have bonded with the same female, they fight viciously over her. Sound familiar?

The advantage that a long-term territory holder has over an intruder is subtly different from a home field advantage. The asymmetry for the home field advantage has no asymmetry in the value of the resource. However, the asymmetry for a long-term territory holder refers to a resource asymmetry. The resource is knowledge of his territory. Nectarivorous birds such as territorial sunbirds, *Nectarinia reichenowi*, have a knowledge of the flowers they have visited. Common-sensical sunbirds avoid visiting flowers they have just visited (see Chapter 7). By following this rule, they can minimize flight costs by continually moving through flowers with the most nectar possible and only returning when flowers have renewed their resources. An intruder lacks



such knowledge and would have to acquire information before the payoff from the territory would equal the payoff that the current territory holder enjoys (Kamil 1978). The territory has more value to the resident.

How does the additional knowledge of resource value affect the likelihood of victory through persistence in a war of attrition? A prediction of the war of attrition is that the resident will win more often by persisting longer when the value of the resource is high. The simple asymmetry in the knowledge of resource value gives the resident male an edge in the contest, he knows what he is fighting for. Austad (1983) manipulated the degree to which bowl and doily spiders had information on the value of the female. In some trials he introduced both males onto the female's web at the same time. Males have the same knowledge. In other trials he gave one male, the 'resident', varying amounts of time to assess the female on her web. Male bowl and doily spiders can determine if the female is ready to mate after a few minutes. Virgin adult females are of highest value to a male spider and he can assess her rapidly. After a male has determined that he will copulate he begins charging his pedipalps, the sperm transfer organ in male spiders. Once the male starts copulating he gets diminishing returns from additional sperm that he transfers. Initially, a short period of sperm transfer leads to a rapid rise in fertilization success, but the rise in fertilization success drops as the female's storage organ fills up. Sperm transfer, like many aspects of foraging discussed in Chapter 6, follows the Law of Diminishing Returns and the MVT. Initially, the value of the female to the male is high (Fig. 8.9) and he should be more vigorous in his defense. However, after sperm transfer goes beyond 7 min, the value of defending the female begins to drop off as her organ fills up, and he should be much more likely to yield to an intruder.

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Figure 8.9. The value of the female to male bowl and doily spiders at various times after contact: simultaneous introduction of both males, "resident" has a one minute lead, "resident" has assessed the female as ready for copulation, "resident" has had 7 min of copulation, and 21 min of copulation. The value perceived by the intruder that is introduced at any point during the resident's copulation remains constant (redrawn from Austad 1983).

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Knowledge adds value for the resident and this information has an important effect on the motivation to win for the resident, relative to the

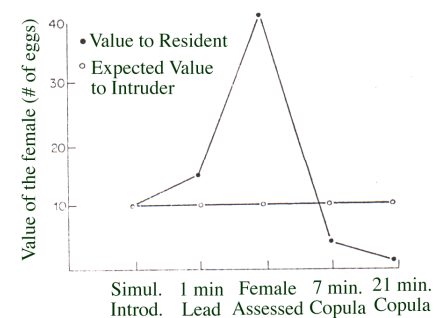
intruder. When smaller residents were introduced to a larger intruder, one would expect the odds to be against the smaller spider. However, the smaller resident won 60% of the contests when the value of the female was high, but only 20% of the contests against the larger opponent when he had engaged in 7 minutes of copulation and he always lost if he had 21 minutes of copulation. This additional knowledge possessed by the smaller competitor gives him a subtle advantage and increases his persistence time during contests.

## The proximate control of aggressive behaviors

### Endocrine regulation via hormones of the brain and gonads

Aggression clearly plays a major role in success during a contest. But aggression is a two-edged sword in that there are clear benefits and costs to fighting. In this regard, mechanisms have evolved that modulate levels of aggression. Aggression is very often restricted to the adult phase and the breeding season. Territorial aggression is often tightly governed by circulating levels of hormones. Given that there are winners in contests and hormone levels might predict winning, what hormonal changes alter the behavior of the loser in the long-term? What causes retreat from contests in the short-term? An understanding of the neuroendocrine bases of behavior is necessary to understand these issues of contest and conflict.

No hormone receives more attention in popular press as an aggression-inducer than the gonadal steroid testosterone. In males, testosterone is secreted in the testes in response to gonadotropin, a protein hormone, which is produced by the anterior pituitary. The anterior pituitary is an

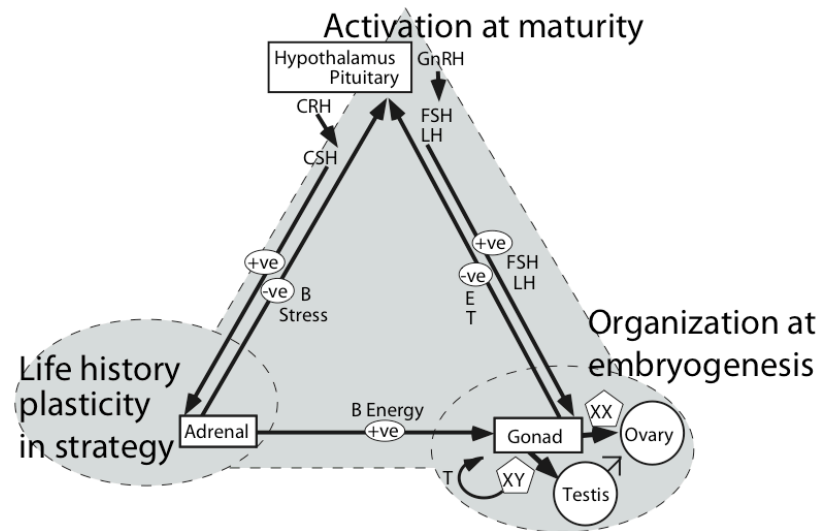


important control region of the brain that produces a many behaviorally relevant hormones. Testosterone is also involved in a classic negative feedback loop in which higher levels of testosterone produced by the testes will cause gonadotropin secretion by the brain to be suppressed. Given the interaction between gonadotropin control of testosterone, and vice



versa, it is not surprising that gonadotropins such as Leutenizing Hormone (LH) can alter male aggression. LH has also been linked to displays of aggression, which by virtue of the sheer size of the combatants, are more than intimidating to human observers. Male elephants enter a behavioral state known as **musth** during the breeding season in which aggressive charges to rivals are common. Injection of LH into sub-adult male elephants appears to trigger this behavioral state as well as a concomitant rise in plasma testosterone (Lincoln and Ratnasooriya 1996). In males, testosterone seems to increase the likelihood that behaviors are expressed, but it is important to realize that testosterone does not directly control specific behaviors (Feder 1984; Moore 1991)]. Testosterone and protein hormones such as LH that modulate Testosterone can be considered one of the many factors that contribute to the heightened **arousal** that is associated with aggression.

Figure 8.10. Schematic of interactions among endocrine organs of the brain (highlighting the pituitary-hypothalamus), gonads, and adrenal organs of an archetypical vertebrate illustrating the regulatory (positive and negative) pathways governing the endocrine system.



Testosterone influences a diverse set of behaviors in males. However, contrary to popular belief that the ‘male hormone’ is testosterone and the ‘female hormone’ is estrogen, testosterone has potent effects on females, even though most female vertebrates appear to have far lower levels of testosterone than males. In females, the low levels of testosterone promote many female behaviors and appear to be responsible for female sex drive (Wingfield and Moore, 1988). It is also not the case that testosterone is invariably related to aggression. Groups of white-browed sparrow weavers breed in cooperative groups and participate in defending their communal territory from other groups. Territory defense involves regular boundary patrols that are punctuated by a characteristic

chorus singing elicited by all group members in concert. Wingfield and Lewis (1993) simulated territorial intrusions by placing a caged group within a territory and playing back tape-recorded choruses through a speaker placed adjacent to the cage. The target group responded with a dramatic increase in territorial aggression by all group members. Plasma levels of testosterone were not elevated during intrusions. However, plasma levels of LH were elevated in breeding females after challenge. This suggests that aggressive behavior in females may not result from

elevated testosterone, but from the upstream effects of LH.

Despite these important exceptions to the role of testosterone in promoting aggression, testosterone has a broad spectrum of effects that also serve to enhance the physical abilities of males in particular. The tissues of the muscular system and brain appear to be the most important targets of testosterone action with regards to contests. Human experimentation with the drug has led it to be banned as a performance enhancer in Olympics and other athletic competitions. Muscles enhanced by testosterone are not just the skeletal muscles that promote strength. Testosterone also has effects on many muscle systems that are sexually

dimorphic with respect to males and females. For example, testosterone is in part responsible for triggering the development of special sound producing muscles in male fish (Bass 1996), and amphibians (Kelley and Gorlick 1990).

Testosterone not only triggers the development of vocal structures, but it is also responsible for sensitizing certain targets in the brain and thus increases the likelihood of song (Johnsen 1991; Ketterson and Nolan 1994). In free-living red-wing blackbirds, *Agelaius phoeniceus*, natural variation in the rate of song production on their territories is correlated

with the level of testosterone circulating in their plasma (Figure 8.11). Cause and effect between testosterone and the propensity to sing songs has been revealed in experiments that elevate levels of plasma hormones with implants. Implants are semi-permeable membranes surrounding the hormone of interest, in this case testosterone, which is released into bloodstream in a timed-release fashion. Dark-eyed juncos, *Junco hyemalis*, that receive an implant with testosterone, sing songs at more than twice the rate of sham-manipulated birds that receive an empty implant (Figure 8.12). In experiments described below, it is clear that the intensity of song, and the way in which songs are directed at rivals is very important in transferring information during territorial contests.

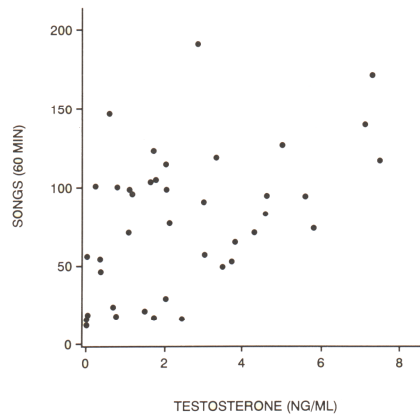
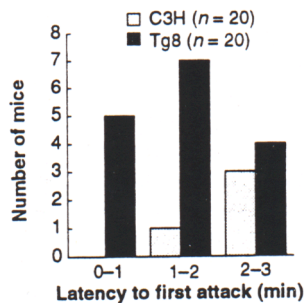


Figure 8.11. The rate of song production in free-living redwing blackbirds, *Agelaius phoeniceus*, is positively correlated with plasma testosterone concentrations. Song production was recorded on their territories (Johnsen, 1991)

Figure 8.12. The effect of experimentally elevated plasma testosterone on rate of song production by dark-eyed juncos,

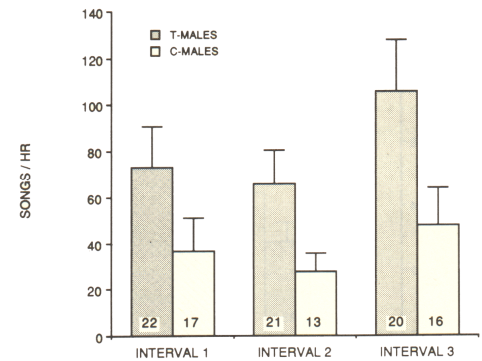
*Junco hyemalis*. The three intervals refer to periods of the nesting cycle when hatchlings were 0-3, 4-7, 8-10 d olds. From Ketterson and Nolan (1994).



## Neuropeptides and aggression

The notion that the proximate regulation of aggression is only governed by the endocrine system of vertebrates is of course overly simplistic. New studies have linked single genes directly to elevated aggression in humans. For example, males in a Dutch family line display abnormally high levels of aggression suggesting a genetic cause to the behavior (Brunner et al. 1993). This particular family also showed a striking deficiency in the enzyme monoamine oxidase A (MAOA), which degrades serotonin and norepinephrine in the brain. These two compounds are potent neurotransmitters that are responsible for carrying the electrical activity that travels along a neuron across the synapse, which is the space between the contact point of two adjacent neurons. The signal traverses from neuron to neuron, not by electrical activity but by neurotransmitters. The gene MAOA and another related enzyme MAOB are present on the X chromosome, so males possess a single copy of the gene. Any mutation of the gene would be expected to have a far larger effect on males compared to females, which carry two copies. Females in the Dutch family showed normal levels of aggression because they are likely to possess another functional copy of the gene MAOA on the other X chromosome.

Figure 8.13. Comparison of the latency of 'resident' male mice strains to attack an intruder placed in their home cage. The C3H strain of mice is a control line. The Tg8 strain, which has gene MAOA deleted, has a much shorter latency to attack intruders.



Recently, Cases et al (1995) have generated a mutation for the same gene in a line of mice to test for the generality of the role of MAOA in controlling levels of aggression in other vertebrates. Males with a deficiency in the gene displayed far higher concentrations of serotonin and norepinephrine in their brains suggesting that the defective MAOA

was not degrading the neurotransmitters but instead allowing the neurotransmitters to ‘pool’ up in the brain. In addition, the genetic lesion greatly enhanced the tendency of a resident mouse to attack an intruder when tested in their home arena.

It remains to be determined if variation in the gene for MAOA is indeed responsible for natural variation in aggression among males, or perhaps females, in free-ranging vertebrates. Promising work on serotonin, the molecule that is degraded by MAOA, suggests that it might play a role in modulating the effects of social agonistic interactions in both dominant and subordinate Damsel fish (Winberg et al. 1996). Recent advances in molecular tools such as those used to identify the gene MAOA, will hasten the quest for genetic causes of aggression that arise from alterations of the nervous system. Ever since the techniques of radioimmunoassay were developed by the Nobel Laureate Rosalyn Yalow in the 1960’s, our knowledge of the role steroid hormones play in promoting behaviors in natural populations has expanded tremendously. Perhaps, with the advent of new molecular tools, we will see a similar renaissance in our understanding of the genetic and molecular bases of aggression and propensity towards hawkish and dove-like strategies.

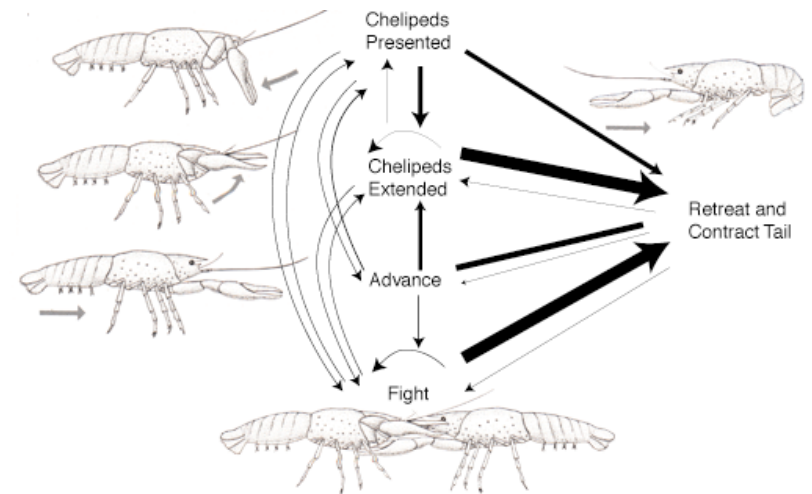
### Fight and Flight and the Nervous System

The fact that deletion of a simple gene, MAOA, causes increased aggression does not imply a single gene causes aggression. Genes act through a number of proximate mechanisms, such as the action of neurotransmitters like serotonin at a neuronal synapse. Neurons might change during development to yield different outcomes, different sensitivities to neurotransmitters, depending on experiences of early life.

Winners in agonistic contests may become more hawk-like in their territorial posturing and losers may become more dove-like due to soft-wired changes in the nervous system. Work on the changes in individual neurons of animals, which are engaged in long-term social interactions, demonstrates that neural circuits can be modified, thereby modifying aggressive behaviors. Recent work on the crayfish nervous system has identified a simple circuit responsible for changes in hawk-dove behaviors.

Crayfish have a system of escalating contests in which the chelipeds, which are large crushing claws, are presented and then extended. The cheliped is a formidable weapon and when extended is usually enough to send the opponent into a retreat, even if both combatants are behaviorally dominant (de Roth 1974; Rubenstein and Hazlett 1974). Retreat during the extremely dangerous battles of crayfish is accomplished with the muscular tail. If the crayfish is threatened, the tail contracts, and the crayfish is propelled backwards out of harms way. If you observe fighting crayfish the most common behavior you find is the retreat behavior (Fig. 8.14). The tail flip and retreat is an important component of the agonistic rituals between dominant crayfish. Retreat in fighting crayfish is the better part of valor. Retreat in crayfish is due to a “soft-wiring” by the nervous system, in that the tendency to retreat can be accentuated or suppressed depending on social experience.

Figure 8.14. Frequency of transitions between escalated display behaviors in which chelipeds are presented, extended, or advanced for fighting. The width of the arrow is proportional to frequency of transition between pairs of behaviors. The most frequent behavior in fighting crayfish is retreat! Redrawn from



Drickamer and Vessey (1986).

The muscular tail contracts rapidly in response to neural input from the

lateral giant (LG) neuron. By virtue of its extremely large diameter, the giant fiber can conduct nerve impulse from the brain at high speed (Krasne et al. 1997). When dominant crayfish engage in contests, any level of escalation will trigger the retreat behavior with a high frequency (Krasne et al. 1997). Retreat followed by advance and further posturing with the chelipeds is an important loop in the ritualized contests of crayfish. In contrast, subordinate crayfish are wary of attack at all times and tend to stay clear of agonistic encounters. Rather than fire escape neurons all the time, the LG neuron of subordinate crayfish is suppressed. They tiptoe around and stay out of trouble. If subordinates retreated too often, they might hurtle backwards into the crushing claws of a dominant crayfish. Crayfish live at very high densities.

The differences in escape reflex behavior between dominants and subordinates arise from the relative excitability of the LG neuron. At rest when no agonistic interactions are occurring, excitability of the LG neuron seems to be independent of social status. Both dominants and subordinates are capable of executing the tail flip (probably in response to predators and not necessarily competitors). However, during agonistic encounters the excitability of the LG neurons reflex declines substantially in subordinates, but only slightly in dominants. Because dominants often engage in offense, retreat is a natural counterpart to the ability to attack, particularly in an animal with lethal fighting capability.

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Figure 8.15 Full page drawing (not ready for production yet) of the lateral giant neuron system of a crayfish with a blow-up view of the neurons, the gap junction, and two alternatives: 1: serotonin type 1 receptors that capture the serotonin and transmit the signal to trigger the tail flip, 2: serotonin type 2 receptors that capture the serotonin and block the transmission of the signal to the trigger the tail flip.

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The single change in the state of the neuron is a classic example of plasticity in fighting behavior. An individual crayfish is not fixed with regards to flight or fight during its life time rather changes in a single neuron can lead to different tendencies. The reversibility of the tail-flip response is due to a change in the kinds of receptors that cover the neuron. Receptors are protein molecules found on the outer surface of neuronal cells that intercept the neurotransmitter serotonin that traverses the synaptic gaps between neurons (see Fig. 8.15). Applying serotonin to

the LG neuron of socially dominant crayfish enhances the response of the tail flip command neuron to sensory stimuli in socially dominant crayfish. In contrast, applying serotonin to the LG neuron of subordinates inhibits the response of the tail flip (Yeh et al. 1996). The LG neurons in socially dominant crayfish are surrounded by a population of cells with a specific type of serotonin receptor that captures the serotonin and transmits the nerve impulse to the LG neurons, which results in the tail flip. In contrast, the LG neurons in subordinate crayfish have populations of LG neurons, which have a second type of receptor that capture the serotonin but does not transmit the nerve impulse to the LG neurons. One set of identical neurons in dominants and subordinates, coupled with subtle changes in the proteins embedded in the cell membrane of the neurons, can alter a qualitatively different behavior that is important in agonistic encounters.

The ability to turn on a different kind of behavior depending on social environment is only one way the flight or fight response can be modulated. The behavior of lizards is very sensitive to the effects of their own body temperature (Huey 1982). Contrary to popular notion, many lizards like to operate with a body temperature very close to human body temperatures -- 35-40°C. They are often alert, hot, and fast. Lizards being ectotherms receive their heat from the sun and thus are cool at night but hot during the day. A lizard that is too cold cannot sprint very quickly. The body temperature of the lizard triggers the alternative fight or flight response. Huey and Hertz found that lizards with a cold body temperature were much more likely to turn around, face the threat, and adopt an aggressive response. When warm they would simply flee. The difference in behavior within the same individual is so rapid it may be controlled by the sensitivity of the nervous system to temperature. It has not yet been determined whether lizards change their aggressive posture in contests between opponents as a function of temperature, but it does alter anti-predator tactics.

### **Testosterone and Corticosterone modulators of Status and Stress**

Many species appear to exhibit differences among individuals in propensity to win or lose. We tend to dichotomize individuals as dominant if they are winners and subordinates if they are losers. A winning record is likely to initiate further contests over resources and

maintain high dominance status. In contrast, a history of losing agonistic contests is likely to result in avoidance behavior towards agonistic situations. The mode of action for generating winners and losers can reside within the nervous system. Winners and losers can learn to be winners and losers. Winning and losing can also be modulated by the endocrine system. The effect of contest histories on the propensity to be a winner or a loser has been shown in the American goldfinch, *Carduelis tristis* (Popp 1988), the great tit, *Parus major* (Wilson 1992), and the Siamese fighting fish, *Betta splendens*, (Bronstein 1985).

Changes in aggressive behavior may be mediated by a positive feedback relationship with testosterone (Ramenofsky 1984; Baptista et al. 1987). When pairs of male green anoles, *Anolis carolinensis*, are placed in staged contests in the laboratory, the winner's plasma testosterone becomes elevated relative to the losers (Greenberg and Crews 1990). Plasma testosterone concentrations in all species of lizards are not universally affected by victory. There is no evidence of elevated plasma testosterone levels in tree lizards, *Urosaurus ornatus*, when they have engaged in either short aggressive encounters (Thompson and Moore 1991; Knapp and Moore 1995; Knapp and Moore 1996) or longer term 7-d encounters (Knapp and Moore 1995). Evidence from studies of the tree lizard suggests that testosterone only acts during early hatchling development and these early changes seem to hardwire levels of aggression. Tree lizards come in two throat color morphs; blue-throated males are behaviorally dominant to orange-throated males. Manipulating levels of plasma testosterone in hatchlings can alter the frequency with which hatchlings develop into aggressive blue-throated males or subordinate orange-throated males (Hews et al. 1994).

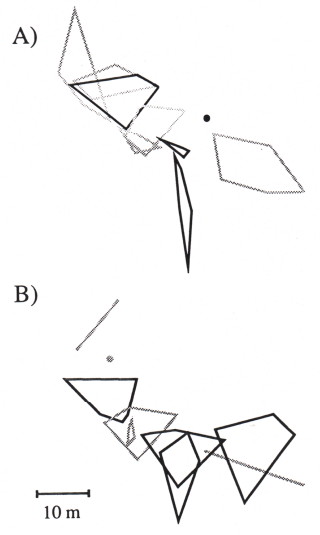
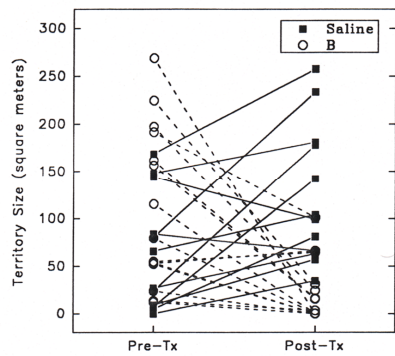
Glucocorticoids comprise another potent class of steroid hormones that are secreted by the adrenal glands. The adrenal gland is also responsible for secreting a number of potent neurotransmitters, such as adrenaline, which is clearly involved in fight or flight responses. Corticosteroids appear to have much longer lasting effects than the neuropeptides on propensity to display flight versus fight behaviors. In addition, corticosteroids have important effects on physiology and appear to be vital for survival (Sapolsky 1992). Glucocorticoids have an important role in restoring glycogen levels in vertebrates after heavy activity (Kraus-Friedman 1984), such as might arise in contests. Thus, when

corticosterone is elevated in short-term encounters, it probably has an important effect on energy metabolism (Miles et al. 2007) rather than effects on behavior per se. For example, corticosterone is elevated in males that win short-term contests in tree lizards.

It is important to distinguish between the effects of corticosterone at short versus long time scales. Elevated corticosterone levels have been observed in subordinate baboons following long-term interactions with dominants (Sapolsky 1982). In the hamster, stress from social interactions elevates corticosterone levels, which in turn deactivates specific neurocircuits in the brain that are linked to aggression (Kollack-Walker et al. 1997). Male tree lizards appear to maintain high levels of corticosterone if they lose a long-term encounter compared to the winner of such a contest (Knapp and Moore 1995). As suggested by the involvement of corticosterone in the long-term stresses of social interactions, glucocorticoids are also classically known as the stress hormones (Johnson et al. 1992). Levels of corticosteroids rise during many stressful events, not just those that arise from social interactions. However, chronically elevated corticosterone delivered in hormone implants appears to suppress aggressive behaviors in lizards (Tokarz 1987; DeNardo and Licht 1993) similar to the suppression of aggression following chronic loss in long-term territorial encounters between a dominant and subordinate (Knapp and Moore, 1995). Given the broad spectrum of effects that corticosterone might have, it is important to carry out experiments that attempt to uncouple the physiological effects of corticosterone on behavior from the social effects of stress that might occur in natural populations. Very often subordinate animals are defined by their inability to hold a territory.

What causes a suppression of aggression and territorial behavior in subordinates? Do the effects of corticosterone on aggression have a direct effect on the ability of a male to hold a territory in the wild? Implanting territorial male lizards with timed-release capsules of corticosterone can test this hypothesis (Moore 1986; Moore 1988; DeNardo and Licht 1993). A control for the effects of the surgery would be to put an empty implant into males on adjacent territories. In the wild, males with corticosterone implants lose territory when competing against males that receive a sham-implant. Corticosterone appears to strongly suppress territorial behavior of lizards (Fig. 8.16, 17).

→Figure 8.16. Effect of corticosterone implants and sham implants on territorial behavior of male side-blotched lizards, *Uta stansburiana*. Half of the males received corticosterone (grey territorial boundaries) and half received sham implants (solid boundaries). The territory size of all corticosterone implanted males shrinks from pre-treatment territory size (A) to post-treatment territory size (B), while the territory size of sham-implanted males expands (DeNardo and Sinervo 1994).



←Figure 8.17 Change in territory size before and after treatment for corticosterone and sham implanted male side-blotched lizards. Corticosterone implanted males lose territory while sham-implanted males gain territory (DeNardo Sinervo 1994).

Proper controls for this experiment must demonstrate that chronically elevated corticosterone does not cause males to patrol their territories at lower frequency simply because corticosterone extinguishes territorial behavior. Are males that receive corticosterone shrinking their territories because corticosterone suppresses their territorial behavior? Alternatively, are corticosterone males losing their territory to their sham-implanted neighbors, perhaps because corticosterone lowers a male's motivation to defend a territory against a more aggressive sham-implanted rival. If corticosterone implanted males lose territory to rival sham-implanted males because of an asymmetry in motivation then eliminating the asymmetry (e.g., sham-implanted rivals with normal aggression) would allow corticosterone males to defend a normal-sized territory. Implanting corticosterone into all males on an outcrop should have no effect on territory size of corticosterone implanted males if

corticosterone really only lowers the behavioral state of arousal.

To test this idea, DeNardo and Sinervo (1994) implanted all males in a neighborhood with corticosterone. This important control has the predicted effect -- when everyone has the same state of arousal no one wins and no one loses. There is a clear demonstration of territorial pressure. In the first experiment, males were asymmetric in their steroid profiles, and sham-implanted males win space at the expense of corticosterone-implanted males. Remove the asymmetry and no one wins or loses ground even though everyone in the neighborhood is now a "stressed-out" subordinate.

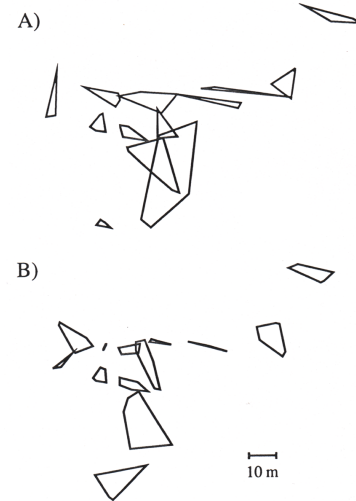


Figure 8.17 Manipulation of an entire neighborhood of male side-blotched lizard with corticosterone implants causes everyone to experience the same lowered level of aggression. Because every pair of neighbors is symmetrical in aggression (low), there is not a net change in territorial boundaries before versus after implantation of corticosterone. From DeNardo and Sinervo 1994).

## Cognition and Communication During Contests

### Acquiring Information about Resource Holding Power

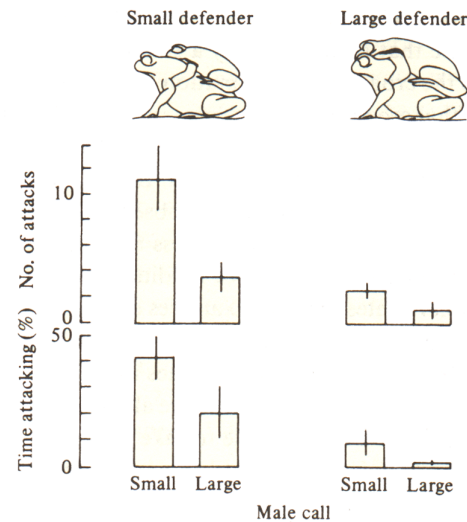
Most competitors are **asymmetrical** in their fighting ability. The asymmetry might arise from some neuroendocrine cause in motivation. Alternatively, individuals may vary in their physical ability to hold onto the territory -- some are more capable fighters. Differences in prowess or the ability to hold on to a territory is called **Resource Holding Potential (RHP)**. How do animals gain information on RHP of opponents during contests? Hormones clearly play a role in the development and expression of aggression. Likewise, relatively simple

neuronal switches can alter the basic behavioral patterns underlying aggression depending on past success in contests. However, not all agonistic behaviors are reflexive or driven by the endocrine system. Many behaviors might be derived from cognitive events that rely on the detection of asymmetries in the physical capabilities of opponents. Size asymmetries in contests should be relatively easy to detect. For example, spiders might be able to detect the relative size of an opponent by how hard the opponent plucks at the territory holder's web. Thus one of the most universal advantages in conflicts of strength is the relative size of the combatants. Relative size could be considered a straightforward measure of RHP.

Toads communicate information on RHP based on size via the pitch of their croak (Davies and Halliday 1978). Toads engage in amplexus behavior in which a male clasps the female from behind and then guards her while he waits for her to oviposit in the pond. Unpaired males that attempt to dislodge the 'resident' from the female's back and this intruder often attacks the amplexing male. The amplexing male uses force to intimidate the attacker by pushing against him with his feet, but he also croaks in an attempt to vocally intimidate the rival.

Playback experiments have been used to show that the croak is involved in male assessment. An intruding male that hears a deep croak played from a loudspeaker is much less likely to attack a small male than if he hears a higher pitched croak. Even large males gain some measure of protection from a deep croak (Fig. 8.18), however, a large male is much less likely to be attacked than a small male suggesting that the intruding male does not just use croak depth to assess the amplexing male's size. Perhaps the intruder gains additional information on a male's size during the wrestling matches in which he attempts to dislodge the male from the female's back. The defender pushes vigorously to avoid being removed from the female's back. The deep-croak signal means that the amplexing male is large and size is related to RHP. The deep croak might be enough to intimidate a rival from even initiating the wrestling match.

Figure 8.18. A deep croak serves to deter attacks from other toads in *Bufo bufo*. A small defender receives fewer attacks when deep sounding croaks are played by a loudspeaker to unpaired medium-sized males that are attempting to usurp



control of females from the 'resident' amplexing male. Even large defenders experience some measure of protection from the size of the croak. The actual defenders in these trials had their mouths held closed by a rubber band to avoid the confounding effects of their croaks during playbacks (from Davies and Halliday, 1978).

Another example of RHP communication includes "roaring" in red deer (Clutton-Brock and Albon 1979). In playback experiments, male stags that are presented with a

red deer recording that plays for an unusually long time are more intimidated than males presented with a normal bout of roaring. Deer interpret the length of time that a male can roar as an index of RHP, and better condition is presumably required to be able to roar for a long time. In a similar fashion, male coal tits appear to be intimidated by males that sing ever-escalating songs that extend beyond the normal length (Adhikerana and Slater 1993).

### Badges of Status and Advertising

The prediction that animals in contests should not reveal their intentions was derived from the **symmetrical war of attrition**, although this prediction was valid only under very restrictive conditions. In particular this was a symmetrical game in which the combatants were equally matched in ability and resource value. Revealing intent was not evolutionarily stable, since cheaters using 'cheap talk' could exploit it. If a cheater could detect intent, then it could try to bluff its way out of the contest by exploiting the information to its advantage. You can think of the value of keeping thoughts to your self in a game of poker or indeed in any "parlor game" where information changes your strategy during the game. When you get a royal flush or four-of-a-kind, it is important to maintain a "poker face" so that you can soak your opponents for as many poker chips as possible. It does you no good to reveal your

intentions by making one enormous bet on that round. Players try to get bets going slowly so as not to reveal intent. Likewise, animals should conceal intent, which would give their opponent an upper hand.

Like a game of poker, as a contest between two animals unfolds, the contestants accumulate information about the opponent. Once enough data has been collected, a male may decide to end the contest and flee, or escalate to the next stage of the contest to acquire more and more information. Different displays and levels of escalation may be useful to measure different attributes associated with fighting ability. Diminishing returns of sampling a single class of displays leads to an escalation of the next display from which more information about the opponent may be gleaned (Enquist and Leimar 1983; Enquist et al. 1990). Because contestants are unlikely to reveal information, combatants are literally probing each other for weaknesses regarding the opponents RHP.

While the rule-of-thumb is to withhold information about intent in symmetric contests, such strategies do not hold in contests with asymmetry. In asymmetric contests a male that has a mating type that is stronger than the other, might be expected to "advertise" this skill by some sort of **badge of status** (Maynard Smith and Harper 1988). By walking around and displaying this badge of status, a very dominant individual could avoid most contests because other males would be unlikely to challenge such a powerful or skillful male. By avoiding unnecessary contests, the dominant individual could focus on contests with other more equally matched individuals, which are likely to lead to a war of attrition. Therefore, advertising may be necessary for the dominant strategy even though the simple war of attrition models suggest otherwise, because the dominant can avoid many contests.

Maynard Smith and Harper (1988) modeled the use of badges in contests and found that badges should be costly to produce and thus they should give an honest indication of a male's general physiological vigor that would likewise be translated into prowess in contests. "Bluff" signalers should incur a cost when they signal high status, but do not have the RHP to back up their cheap talk (Møller 1978; Rohwer and Rohwer 1978), or the signal places them at greater risk of predation.

Badges of status have been investigated in a large number of taxa. Very

often pairs of contestants, or dyads, are tested in experimental arenas, and the level of aggression of the two contestants is assessed. A general prediction from game theory is that contestants with the same level of intensity in their badges should be equally likely to win contests. The two might be expected to escalate the conflict. In contrast, contests between asymmetrical opponents, which differ in their badge (e.g., presence or absence), would be expected to determine the outcome of the contest more quickly -- one will win and the other will retreat.

These expectations are borne out in species of lizards that commonly have differences in their throat color. For example, in the tree lizard, *Urosaurus ornatus*, which is common in the desert southwest of the United States, males have throats colored with either orange, yellow, blue, or the blue patches on their throats are ringed with orange (Thompson and Moore 1991; Thompson and Moore 1991). Males with blue throats ringed with orange are behaviorally dominant to the other throat color morphs. Males with solid orange throats tend to be subordinates. Thompson and Moore used paint experiments to alter the color of the male's throats (Thompson and Moore 1991). They focused their efforts on males with blue-ringed with orange. By matching size and amount of blue relative to orange on throats, they could control for males that were presumably similar in quality and aggression. They then painted one group solid orange, the color of subordinates, and they painted the other group with a blue throat ringed with orange. The males painted with blue throats ringed with orange won nearly all of the contests suggesting that the solid orange on their rival's throat was indicative of a weaker opponent. Thus, the blue-ringed-with-orange signal is a badge of status relative to the solid orange-throated males.

### **Honesty and Deception in Signals**

Badges are common throughout the animal kingdom and animals also display in a manner that predicts future behavior such as their intent. Several models were constructed to explain why such behavior could be evolutionarily stable when they should not reveal much information to rivals. Enquist (1985) proposed a model, nicknamed the 'risk-right' model. This model suggested that cheating is precluded because increasingly effective threat-displays are increasingly costly in terms of the risk of retaliation. Thus, only individuals that are actually prepared



to pay a high price of retaliation can afford to use highly effective displays. This model predicted that display types, which are increasingly effective in winning disputes, are also increasingly likely to cause retaliation. Another model by van Rhijn and Vodegel (1980), suggests that cheating is precluded because **individual recognition** will allow the detection of cheats, and will select against cheating. Many animals display some form of neighbor recognition. In the next section we will explore the role of badges in individual recognition systems -- one of the basic cognitive ingredients for assessment. Badges must be honest if the probability of a contest is high. Combatants will have to put up or shut up once they are challenged.

If a mating system evolves individuals with badges of status advertising their prowess, the situation is ripe for an interesting strategy to evolve that can exploit this information in some way. It is not necessarily possible to evolve a stronger strategy, which would entail additional costs associated with the development of more "firepower". Individuals who wear a badge of status may have some other kind of weakness that could be exploited, perhaps in their perceptual system. Many males continually harass males with badges, given that they hold onto valuable resources. The evolution of **female mimicry** in males is undoubtedly related to the exploitation of the information embodied in a badge of status, and an ensuing weakness that accompanies badge holders. Rather than fight, the sneaker uses a **deceptive strategy**. We will consider the example of sneaker males in Chapter 9 and general communication theory in Chapter 13. Sneaker males are not using **dishonest signals** during their 'contests' with dominant males. Sneakers use **deceptive signals** and often mimic females in order to disguise their true identity.

### Badges of Status and Hunger as the Great Motivator

The bird the great tit, *Parus major*, is widespread in Europe and has been used extensively by students of animal behavior investigating the role of badges of status. The great tit possesses a dark ventral stripe that is quite variable in width and has been correlated with dominance interactions (Maynard Smith and Harper 1988). Interestingly, males and females both possess a prominent stripe, but the male's stripe is greater in area (1067 mm<sup>2</sup>) than the female's stripe (667 mm<sup>2</sup>). Both sexes appear to use the stripe in status signaling (Maynard Smith and Harper,

1988). The stripe mediates success in dominance interactions of winter-feeding flocks of great tits in both of the sexes. However, the stripe also appears to be used by females as a badge to establish territories later in the nesting season. In contrast, the stripe is paradoxically unimportant to males that likewise engage in vigorous territory defense during the breeding season (Wilson 1992). Females that pair with territorial males have a significantly larger ventral stripe (753 mm<sup>2</sup>) than females that did not become paired (671 mm<sup>2</sup>). Males that successfully established territories (1111 mm<sup>2</sup>) did not show a significant difference in ventral stripe area compared to males that were unsuccessful in obtaining territory (1125 mm<sup>2</sup>).

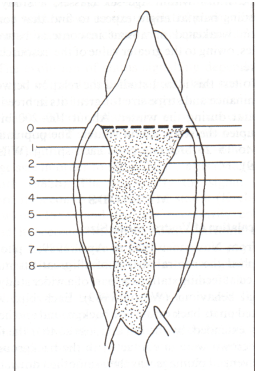
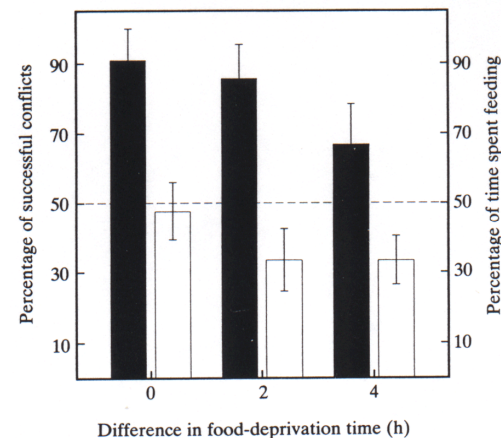


Figure 8.19 Ventral view of a great tit, *Parus major*, showing the dark stripe. The area of the stripe is easily computed from several width measurements, and the ventral stripe can be manipulated by dying the lighter area surrounding the stripe with a dark stain (Wilson 1992).

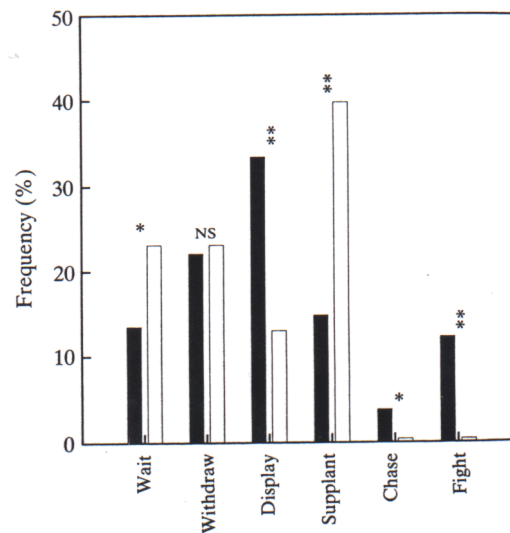
Figure 8.20. Birds with experimentally enlarged ventral stripes most often win contests between unfamiliar tits, which indicates that the stripe is a



badge of status. However, experimental birds won fewer contests (black bars) and fed less (open bars) when confronted by a strange challenger that is motivated by hunger. If the experimentally enlarged ventral stripe was not a badge of status, birds would be expected to win contests with equal frequency (From Lemel and Wallin 1993).

Lemel and Wilson (1993) used black dye to manipulate the width of the ventral stripe and thus test the role of the stripe in modulating contests. They focused their efforts on the winter-feeding flocks of great tits. Lemel and Wilson were particularly interested in the role of the ventral stripe in contests between birds that are strangers (from different flocks) compared to contests between familiar birds (from the same flock). They were also interested in how the motivational state might influence the likelihood of success in a dominance interaction. Hungry birds should be more motivated to win a contest even if the bird was a known to be subordinate and the other contestant was a dominant bird.

Figure 8.21. Frequency with which different behaviors were used in encounters between great tits in an arena in which pairs of familiar birds (open bars), or pairs of strangers (dark bars) interact. Differences that are significant at 0.05 and 0.01 are denoted by \* and \*\* respectively. Strange birds use a less escalated set of behaviors and display the ventral stripe with a far greater frequency than familiar birds. In contrast, familiar birds were far more likely to escalate the conflict to supplanting attacks. From Lemel and Wallin (1993).



In an experiment between strangers, they tested whether birds with experimentally enlarged ventral stripes won more staged contests with unfamiliar challengers. The birds again contested a food resource. Lemel and Wilson varied hunger level of the birds by withholding food for a set amount of time. When strangers were not hungry the bird with the experimentally enlarged stripe won 90% of the contests, indicating that the ventral stripe is a badge of status. However, the bird with the experimentally enlarged stripe won fewer contests and fed less at the food resource, when the challenger was motivated by hunger. As predicted, hunger level was a great motivator, and the subordinate could win contests over less hungry dominants.

Lemel and Wallin also compared contests between strange and familiar birds. Strange birds used displays of the ventral stripe in contests more often than did familiar birds (Figure 8.21). In contrast, familiar birds escalated to the much more aggressive supplanting attacks compared to birds that were strangers. Lemel and Wallin interpret the difference between familiar and strange birds in terms of the confidence in conflict outcome. Individual recognition may be very important in modulating contest outcome among birds with a prior knowledge about resource-holding potential. 'Familiarity appears to breed contempt for a badge of status and birds use other information to win.

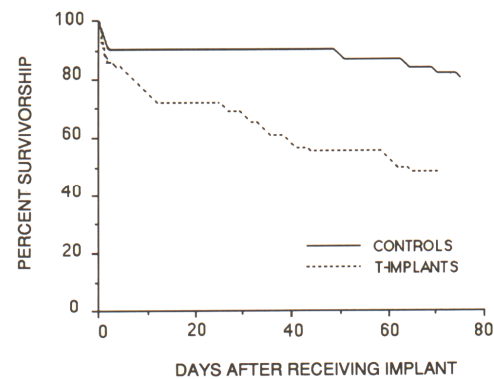
### The Costs of Advertisement and Aggression

Badges of Status gives a male a tremendous advantage in assessment games, but these high RHP strategies are usually not without costs. In vertebrates, male secondary sexual characteristics such as large size, or elaborate ornaments and armaments are usually related to levels of circulating testosterone. Testosterone regulation during either adult (Rand 1990; Rand 1992) or early hatchling development (Hews et al. 1994) appears to be related to the development of alternative throat color morphs in lizards. In addition, expression of badges of status in the side-blotched lizard, *Uta stansburiana*, leads to dramatically shortened lifespan (Sinervo and Lively 1996). Male side-blotched lizards with bright orange sides and throats are behaviorally dominant to males with blue or yellow on their throats. However, the probability that an orange male survives to breed to a second year is only 5% compared to the 25% survival enjoyed by blue and yellow males (Sinervo and Lively 1996). Plasma testosterone levels are 50% higher in orange-throated males compared to blue and yellow males, suggesting a link between the badge and steroids.

Steroids and the development of badges of status have positive effects on dominance, but it appears that steroids also have dramatic negative consequences for other components of the organism's life history. Marler and Moore (1988) have shown that male *Sceloporus jarrovi* lizards that were implanted with testosterone have a reduced survival rate compared to controls in field trials. High levels of aggression that are driven by testosterone may be beneficial in elevating short-term RHP, but an individual may trade-off the advantages of aggression and a

badge with its lifespan. The high costs of testosterone [T] are not merely a pharmacological effect of T-implants. Marler and Moore (1991) ran a second series of experiments in which they provided supplemental food to T-implanted *S. jarrovi* (Marler and Moore 1991). They hypothesized that the males with T-implants were running themselves ragged with continual displays of dominance, spending little time on foraging and feeding behaviors. When the researchers provided T-implanted males with supplemental food, their survival rate improved to levels seen in sham-implanted males. Survival costs of aggression result from an energy trade-off between displaying and foraging. Many of badges governed by Testosterone in vertebrates are likely to be costly.

Figure 8.22. Survival costs of elevated testosterone, the hormone implicated in aggressive displays in lizards (from Marler and Moore 1988).



### ‘Dear Enemy Effect’ and Individual Recognition of Neighbors

Territories are characterized by long-term stability of interactions between neighboring individuals. Over the course of territorial tenure, a resident will have a large number of interactions with their neighbors (McGregor 1993). Territorial interactions are very different from most of the games that we have considered so far where combatants meet for the first time and the contest outcome is determined by a short-term encounter. In territorial encounters, the interactions may be long-lasting and the territorial holders appear to be cooperating. In some cases, the territorial interactions take place over the span of years, which can include the entire lifespan of a long-lived animal (Godard 1991).

The basic experimental paradigm for testing the cognitive abilities involved in **neighbor recognition** is to use a **playback experiment**.

Birds have been extensively tested for neighbor recognition (Temeles 1994). In a neighbor-stranger recognition experiment the researcher typically records the song of a ‘neighbor’ that lives beside the target male. Recordings from a male that lives some distance away are used as a ‘stranger’. The songs from a neighbor and a stranger are played at the border of a territory holder, and the response of the target male is noted (Brooks and Falls 1975; Wiley and Wiley 1977; Godard 1991). The target male’s response to the neighbor’s song is usually less extreme than his response to a stranger’s song. Why is the case? The **dear enemy hypothesis** maintains that once males have established territory boundaries, it is a waste of their time to continue in escalated conflicts with a neighbor. The two exist in a status quo in which they are still assessing one another, but presumably neither is likely to act aggressively because the other male has a home field advantage.

The list of species that have demonstrated some form of a dear enemy effect is found in Temeles (1994). Neighbor recognition in birds is often due to auditory differences among songs of individual males. It is not surprising that raucous and vocal mammals such as vervet monkeys, *Cercopithecus aethiops*, also recognize each others calls (Cheney 1982). It is perhaps only a little more surprising that vocal mammals such as the pika, *Ochotona princeps*, which is a large lagomorph (relative of the rabbit) of the montane Great Basin region of North America, is capable of neighbor recognition (Connor 1985). Pikas are quite communal in that they inhabit rocky hillocks in kin groups and each kin group may be close to other neighboring kin groups. Individual pika might benefit from a dear enemy relationship with other individuals of the same (kin) or neighboring commune (perhaps non-kin). Individual recognition and the ‘dear enemy effect’ in mammals can even arise from olfactory cues that might be found in urine of a the rodent, *Microtus pennsylvanicus* (Ferkin 1988) and of scent produced by a stomatopod, a marine crustacean (Caldwell 1985).

It is not surprising that many birds and mammals show fairly sophisticated abilities with regard to neighbor recognition. Can other vertebrates recognize their neighbors, and what kind of signals do they use to discriminate neighbors? Neighbor-stranger experiments have been performed on lizards. The challenger (stranger or neighbor) is tethered at some point in the target’s territory, and the reaction of the target is

videotaped. Fox and Baird (1992) have found that the target is more agitated in response to strangers than to his dear-enemy neighbor. However, the first set of challenges that Fox and Baird performed were at the territorial boundary. When they moved the neighbor and stranger to the center of the territory, they provoked a marked increase in agonistic behavior for both neighbor and stranger alike. There are certain regions of the territory that appear more heavily defended, even against a dear enemy, and this is the **territorial core**.

### Neighbor Recognition and Spatial Abilities in Weakly Electric Fish

Two groups of freshwater fish, the South American gymnotoids and African mormyrimorphs, are capable of generating an electric signal using the lateral muscles (myomeres) of their bodies. The jolt delivered by weakly electric fish is harmless, but is used to communicate with members of the same species, and also to inspect prey from a distance in the murky waters that they inhabit. The electric organ discharge (EOD) of South American species of weakly electric fish, *Gymnotus carpa*, consists of a ‘pulsed’ waveform with two peaks and two troughs of positive to negative voltage that last about 2 milliseconds (Figure 8.23). McGregor and Westby (1992) investigated two aspects of the cognitive abilities of *G. carpa*: 1) their ability to recognize neighbors, and 2) their spatial abilities to recognize neighbors in the wrong place.

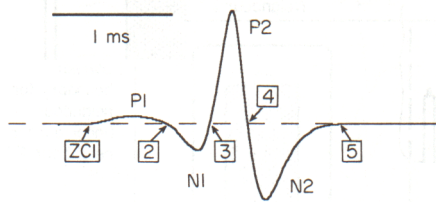


Figure 8.23 Electric organ discharge by weakly electric fish, *Gymnotus carapo*, can be divided in four phases: the electrical potential of the head becomes slightly positive at peak (P1), slightly negative at N1, strongly positive at peak P2, and strongly negative at N2, and then the potential returns to zero. From McGregor and Westby (1992).

Humans can easily visually discriminate among plots of EOD waveforms generated by individual weakly electric fish. Some fish have much more drawn out waveforms with long troughs between the positive peaks (e.g., Fish 3, Figure 8.24), while other fish have very narrow troughs (e.g., Fish 17). Given that we can discriminate these

waveforms by eye, it’s a safe bet that electric fish use the EOD **signature display** to recognize each other.

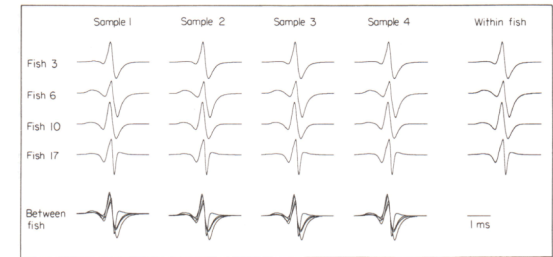


Figure 8.24. Recordings of 4 individual weakly electric fish over a 2-day period. Overlays of waveforms from the 4 fish are different for each time points (bottom row). Overlay of waveforms within individuals (right column) line up.

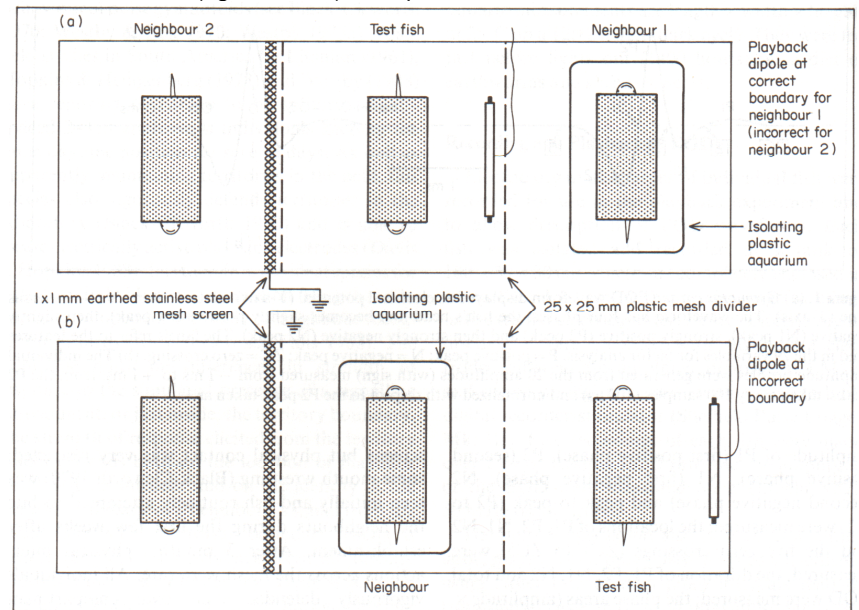
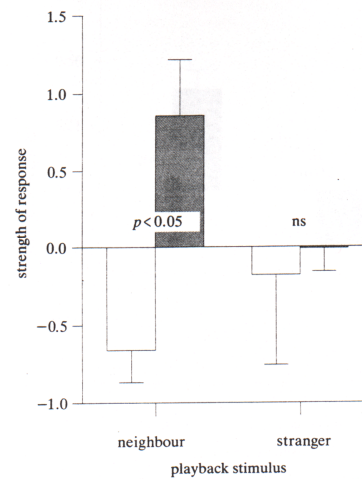


Figure 8.25. Setup for one tank containing 6 territorial weakly electric fish. Recordings of the EOD of neighbors can be played back to a target fish on the correct side (top center) or on the incorrect side (bottom right). While the playback is taking place, the target fish can be “electrically-isolated” from their neighbors. A “Faraday Cage” consists of a narrow gauge stainless steel mesh that can attenuate the EOD felt by the target fish to one millionth of the electrical potential of a full-strength EOD. All 6 fish were also separated by plastic mesh, but they could still interact electrically through the plastic mesh when they were not being tested with playbacks. From McGregor and Westby 1992).

The crucial question is how do we know when an electric fish has recognized another electric fish? What kind of a response might we expect? The response of a resident to the playback of a neighbor's EOD is expected to be quite different than the response of the same resident to the playback of a stranger's EOD. McGregor and Westby (1985) scored the strength of aggressive response as the number of bites to the playback electrode, number of rolls by the fish, and the time of first movement or latency to approach the electrode. From the dear enemy hypotheses given above, we might expect that a neighbor's EOD should elicit a lower level of aggression from the resident EOD. This would be true if we played the neighbor's EOD in the location that the resident would expect to sense its neighbor. McGregor and Westby observed a stronger response from the resident when they played the neighbor's EOD in the wrong place compared to the response towards a strange fish. According to the "dear enemy effect", a neighbor has an agreed-upon border, while a stranger, by definition, does not have an agreed-upon territory border and can come from any direction.

Figure 8.26. →The response of weakly electric fish with a neighbor's electric organ discharge (EOD) is played back on the correct side of the territory (open bar), compared to the neighbor's EOD on the wrong side of the territory. A stranger's EOD was used in a playback on both sides as a control (McGregor 1993).



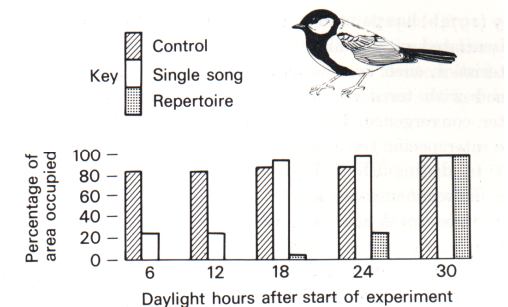
The stranger might be a threat. However, a neighbor in the wrong place is much more threatening. In this case, we might expect a little cognitive "double-take" inside the head of a weakly electric fish: not only does it recognize its neighbor's EOD, but it perceives the neighbor's EOD as emanating from the wrong side of its own territory. The perceived threat to territory tenure is far greater if a neighbor is in the wrong place, as this would only occur if a neighbor were attempting a take-over. When the neighbor's EOD is played in the wrong place, it generates a far more aggressive response than when it is played back in the right place (Fig. 8.26).

### Song repertoire size and "dueling-banjo" song playbacks

For humans, the sound of a bird singing its sweet song seems so peaceful. For the birds, songs are often meant to be a relatively strong deterrent that repulses intruders. A song is often an advertisement of a bird's RHP. Proof of the deterrent capability of songs is provided by removal experiments. When a bird is removed from its territory by the experimenter (Krebs 1977), a speaker placed on the territory that plays the male's song is enough to keep intruders at bay, at least in the short-term. In contrast, an intruder takes over a 'quiet' territory with the resident removed and with no speaker playback. Males have to continuously sing their songs just to keep intruders at bay.

An individual male great tit has up to eight different songs in its **song repertoire** that they will use throughout the day (Fig. 8.28). Krebs has elaborated on the song deterrence mechanisms of birds with an intriguing hypothesis that he refers to as the Beau Geste Hypothesis. This hypothesis was developed after Krebs made natural history observations on territorial male great tits. Whenever the male changed his perch, the male invariably changed his song. Using a different song (e.g., see Fig. 8.27) on a new perch would enhance the illusion that there is more than one male present on the male's territory. The test of this hypothesis entailed a removal of the territorial male, and the speakers were used to playback a single song or a large song repertoire on the empty territory. A control treatment played a non-song sound (tin whistle). Whereas broadcasting a control tin whistle sound was ineffective in keeping out intruders, the single song kept intrusions depressed for 12 h. The addition of song repertoires doubled the keep out time to 24 h. Intruders appear to be more respectful of a territory that has a large song repertoire emanating from it, even if they can't see the male singing the songs.

Figure 8.27. A test of the Beau Geste Hypothesis. A song repertoire (multiple songs) is more effective at deterring intruders than playback of single songs, or a control a tin whistle.



Song repertoires may have even more important uses during communication between neighboring birds. Recent playback techniques have become much more interactive in that the researcher can modulate the kind of song that is played to a target male or the number of songs that might be repeated. The kind and number of songs can be varied in response to the male's song. The woods are a noisy place for males and there may be several males singing in close proximity. How does the male direct his song at a particular male neighbor? Bremond (1968) suggested that **song type matching**, which is a form of singing in which the male matches his song type to a particular male, would allow the male to direct the signal at a particular male on an adjacent territory. In addition, the male could also match the number of song elements that he directed back at the adjacent male.

Figure 8.28. Diversity of phrases used by great tits, *Parus major*, in the Woods adjoining Nottingham, UK. Each phrase consists of a set of notes (see Figure 8.29). These notes are repeated during the course of a single song. No male can sing all 30 songs, rather any one male uses from one to eight phrases, with the average male using three phrases to make up his entire song repertoire (McGregor et al. 1992).

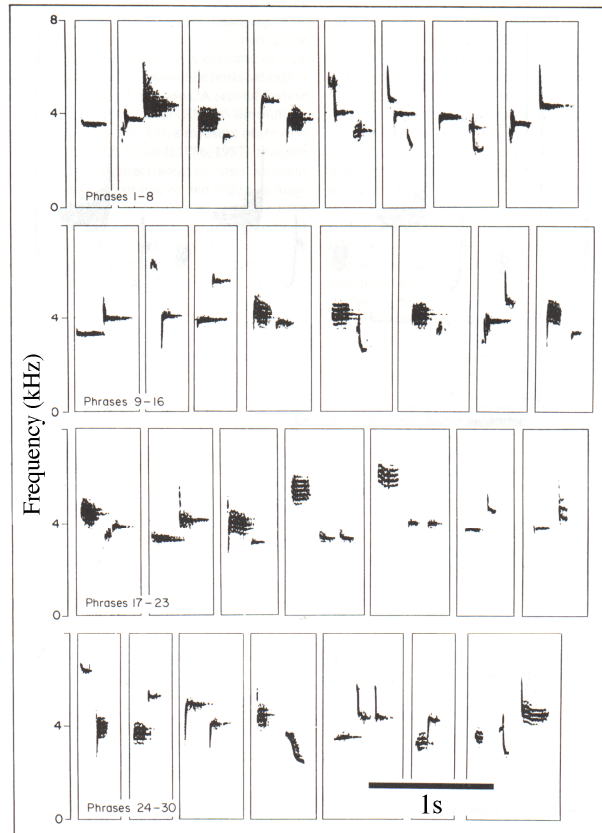
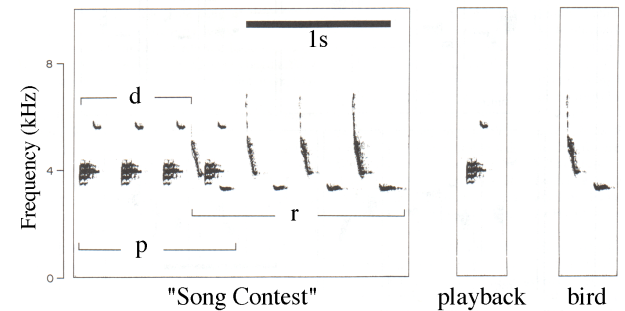


Figure 8.29. "Dueling banjo" contests between a target great tit, and interactive loudspeaker controlled by the researcher. Song contest can be modulated by the researcher playing back one phrase multiple times, p, and the response of the target bird, r, is recorded. The delay between the two songs, d, may have important meaning. For example, as birds escalate to shouting matches the delay becomes negligible and songs overlap extensively.



McGregor and his colleagues found that the targeted male responded best when all components of the song were matched during interactive playback. If the researchers carefully timed the start of playback phrase to coincide with the end of the targeted male's song, they greatly enhanced the response of the target male, suggesting that they had the bird's 'attention'. Likewise, matching the kind of phrase used by the researchers to the kind of phrase used by the targeted male also increased the bird's response to the speaker playback. It appears that matched singing does appear to get the attention of a male. However, the targeted male was not more likely to approach the speaker and escalate the contest. Some other changes in interaction are required to get the male agitated.

This led the team to hypothesize that escalation between males may require an escalation in the song exchange. Much like debaters that get more heated in an exchange, when they start a rebuttal before their opponent has had time to complete their sentence, birds may use overlap to escalate song and thus escalate the contest. One bird overlaps his song with the end of the opponent's song. As the males get more agitated, the overlap of their songs should increase. McGregor et al (1992) found that great tits did respond much more dramatically to overlapping song.

In parallel experiments in European robins, *Erithacus rubecula*, even more dramatic effects of overlapping song were achieved (Dabelsteen et

al. 1997). When overlapping song was used, male robins responded with a quiet twitter song accompanied by posturing. The quiet twitter was not used very frequently with a simple looping playback of song. The quiet twittering is indicative of a highly aroused male (Lack 1969) that might be more likely to engage in a contest. In addition, the latency, or time it took for quiet twittering to begin, was reduced to the one or two song phrases if overlapping song was used. In contrast, it took more than two or more song phrases to elicit quiet twittering when the other two styles of playback were used (simple loop or alternating interactive playback).

Escalation in song contests have also been found to be triggered by accelerating the playback frequency of songs in coal tits (Adhikerana and Slater 1993). Accelerated songs may signal a male's strength or quality. An intruder that is singing an accelerated song may be more of a threat than an intruder with a slower paced song.

Individuals that are confronting one another and participating in a 'dueling-banjo' singing contest, appear to be using the rich set of information that is encoded in songs to alter their behavior. Indeed, in natural agonistic encounters, males may use the information encoded in songs to assess one another and decide to escalate the contest, or to retreat (Enquist et al. 1990). Further research on whether males win or lose contests as a function of the song they sing will lend support to the idea that song is an honest indicator of a male's RHP.

### **Under What Conditions is Dear Enemy No Longer Dear?**

The classic dear enemy hypothesis contends that a neighbor is less of a threat to a male than a stranger, and, thus males respond more vigorously to intrusions by strange males. Certainly, the results from electric fish suggest sometimes the enemy is dear sometimes it is dreaded. Two alternative hypotheses might predict the amount of aggression that the resident would show to an intruder:

1. the relative threat posed by neighbors and strangers,
2. the degree of familiarity a territory owner has with a neighbor.

Consider the two possible outcomes from a neighbor-stranger introduction, if the 'relative threat hypothesis' is governing the behavior

of a territory holder. If the threat is higher from the neighbor compared to the stranger, then the resident will be more aggressive to the neighbor. Conversely, if the threat from a stranger is greater than the threat from the neighbor, the resident will be more aggressive to the stranger. Neighboring males typically have access to females and food and thus the **motivation** to "cross the line in the sand" is low for both males. We can express these ideas in terms of the marginal value theorem with the added twist of risk involved in conflict. The marginal gains that are derived from increasing territory size are not worth the risk of an all out battle with a neighbor. However, if a male bird hears a stranger at the boundary, he must act to turn away the intruder. A targeted male in a playback experiment is typically much more agitated when he hears a strange male's song coming out of the speaker than if he hears a neighbor's song.

The 'degree-of-familiarity' hypothesis is based on the acquisition of information *per se*, and not perception of threat, which might change the motivational state of the resident. Long-term territorial encounters appear to resemble a war of attrition in that contests often involve constant low-intensity exchanges between neighbors. In the asymmetric war of attrition, mistakes during the initial assessment of the opponent can increase the length of contests when they would ordinarily be quite short if the asymmetry is very large (Parker 1984). A resident is quite familiar with his neighbors, but unfamiliar with a stranger. Therefore mistakes are more likely to occur with the stranger (Ydenberg et al. 1989). An increase in the likelihood of mistakes would prolong the contest with a stranger relative to a neighbor. An alternative 'degree-of-familiarity' hypothesis proposes that the function of fighting is to learn (Getty 1989). Because a resident is familiar with his neighbor there is little to learn. In contrast, a resident will fight more often with a stranger because they have to learn whether there is anything to be gained from fighting the strange opponent.

Temeles (1994) performed a comparative test of these hypotheses by comparing the frequency of dear enemy relationships in animals with slightly different kinds of territories. Temeles found that dear enemy relationships were common in animals that defend a multipurpose breeding territory but rare in those that defend a territory that is exclusively used for feeding. In the case of a pure feeding territory, any

neighbor that enters the territory will be perceived as a threat as they could rapidly deplete the resources. However, a neighbor that appears on a multipurpose breeding territory is less of a threat than a stranger, which might attempt a takeover because he is searching for a territory. A neighbor with mates of its own is less likely to attempt takeover.

Temeles found that dear enemy relationships are maintained when risk from strangers is higher (e.g., on multipurpose territories), but dear enemy relations break down when the risk from neighbors is higher (e.g., on feeding territories). Thus, the relative threat hypothesis was supported. In particular, the degree-of-familiarity hypothesis does not predict a qualitative change from dear enemy relations to 'dreaded' enemy relations. The 'fighting to learn' hypothesis may still be operating under these situations because neighbors might be expected to fight more when the value of a neighbor's resource rises relative to its own. The neighbors may be renegotiating the boundaries. While the dear enemy hypothesis is tantalizing, the hypothesis could benefit from more detailed experiments aimed at addressing the various hypothesis within a single species, rather than from comparisons among a large number of quite different taxa (e.g., bees to birds). Such tests await the attention of an eager student of animal behavior.

### **Summary: The Motivation Behind Games**

One of the key features of a game is motivation. Resources provide the potential for enhanced fitness and are the ultimate motivation for many contests between animals. If resources are economically defendable (see Chapter 7) then animals will set up territories to exclude other animals. Priority of ownership is often sufficient to give the territory holder a home-field advantage and deter rivals. Acquisition of information regarding another male's resource holding potential is critical to gain access to defended resources. Animals often use male size as an index of RHP, and communication of size-based RHP entails elaborate side-contests in which two males line up side-by-side or toe-to-toe to assess their opponents size. In the absence of a clear difference in size-based RHP between combatants, the contest is likely to escalate through more elaborate ritualized displays, which can finally culminate in lethal fighting. Game theory suggests that a contestant playing a ritualized contest (retaliator) is often an ESS or *Evolutionarily Stable Strategy* that

is unbeatable, particularly when playing non-ritualized strategies such as dove that never escalates, or hawk that escalates to a fight.

An equally important aspect of the motivation underlying games is the proximate causes of motivation and aggression. The endocrine system of animals serves to promote a behavioral state of arousal that is often associated with the mating season. Both the gonadotropins, which are secreted by the brain, and the gonadal steroids such as testosterone, are important in setting the stage for a number of physiological and psychological states important for resource defense. Aggression can often lead to survival costs owing to the proximate effect of hormones that result in time and energy trade-offs. Thus, equally important are those systems that down-regulate aggression in animals that loose contests. The nervous system (e.g., flight versus fight responses) and the endocrine system (e.g., the stress hormone corticosterone) play roles in promoting less aggressive behaviors. Rather than fight and loose continuously, down-regulation of aggression may promote recovery and enhanced RHP on future contests.

Game theory suggests that providing a rival with information about motivation is not an ESS, because the other individual might exploit the information and prolong the contest. Prolonged battle is a viable strategy for success, particularly in war-of-attrition style contests with escalated signaling. However, the evolution of badges of status in physically vigorous individuals allows them to advertise their prowess and avoid many agonistic interactions, particularly with neighbors. In some situations, alternative male strategies have evolved to exploit the information that a dominant territory holder transmits in a badge of status (see Chapter 9, 13).

Under threat of starvation, it is clear that the motivation of an animal changes and it is less likely to pay heed to a badge of status. Animals are constantly advertising that their territory is occupied, and it is thought that song repertoires may serve an important role in keeping potential challengers at bay. Escalation in conflict may entail the use of song repertoires in which a male matches his song with a territorial neighbor's song to get the neighbor's attention. Animals appear to have sophisticated cognitive capacity for neighbor recognition, and RHP assessment. The neighbor-stranger paradigm serves to test for cognitive



function in both neighbor recognition, and in spatial locations on the territory. If a strange bird is more of a threat than a neighbor, such as on a general-purpose breeding and feeding territory, then a stronger agonistic response is elicited to a stranger compared to a neighbor. Conversely, in the case of territory that serves as a feeding area, the territory holder is often more aggressive to neighbors compared to strangers because neighbors pose more of a threat.

Prolonged contests with neighbors are likely to be costly. Under such conditions a system for achieving a truce, however temporary, may be an important strategic component of games. **Cooperation** is a behavior that occurs between two unrelated individuals that has a net mutually beneficial effect on the *long-term fitness* of both individuals, but the act may entail fitness costs in the *short-term*. Many behavioral interactions may also involve mutualistic alliances. Mutualistic cooperation can be the highest paying strategy under the three conditions: 1) individuals face a low probability of success alone, 2) an individual has a low probability of replacing a partner, and 3) the partners face a large number of interactions before the end of the association. Dear Enemies may reflect such mutualistic alliances. Altruism and mutualism will be explored in upcoming chapters (e.g., Chapter 19).

## Study Questions for Games Animals Play

1. What is the advantage in a ritualized fight? Why is lethal fighting rare?
2. How are badges used in male contest? What are the advantages to a the badge holder?

How are badges used in female choice? What are the advantages to a choosy female?

How are such badges costly? Note: an answer spanning three chapters.

3. The war of attrition suggests that males should not display information or intentions during contests because the other contestant could use it to their advantage. What are some advantages of giving away information during contests?
4. What are the conditions for an ESS? When is hawk an ESS? When can dove invade?
5. List two kinds of asymmetries.
6. Define an endocrine feedback loop (a drawing is quite useful).
7. What hormones are related to aggression? (Describe the action of a reproductive hormone and a neuropeptide). How do other hormones modify these endocrine and neuroendocrine pathways thereby creating regulatory feedback loops (list a steroid and neurological route by which modulation occurs)?
8. What is the dear enemy effect? Give an example.