SIGNAL AMBIGUITY AND THE ASSESSING OF IMPERFECT INFORMATION IN RED-BACKED SALAMANDERS (*PLETHODON CINEREUS)*

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Robert Bryce Page

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Robert Bryce Page

APPROVED:

Dr. Robert G. Jaeger, Chair
Professor of Biology

Dr. Paul L. Klerks
Associate Professor of Biology

Dr. Paul L. Leberg
Associate Professor of Biology

Dr. Susan C. Walls
National Wetlands Research Center

Dr. C. E. Palmer
Dean of the Graduate School

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Chapter 1: COMMUNICATION, SIGNALS, AND IMPERFECT INFORMATION: A REVIEW

RESEARCH GOALS

As the subsequent review will show, communication amongst animals is seldom perfect in the information conveyed between signaler and receiver. Recent results from laboratory studies (Gillette et al., 2000a; Jaeger et al., 2002) imply that red-backed salamanders (*Plethodon cinereus*) may experience situations in natural environments that effectively make ambiguous the chemical signals that salamanders send and interpret, concerning the sexual identity of individuals. Because the communication system of red-backed salamanders has been well studied, this subject represents an excellent opportunity to investigate how ambiguous signals affect patterns of animal behavior. It is my goal to document empirically whether this phenomenon occurs in *Plethodon cinereus.*

INTRODUCTION

Over the past two decades, there has been an increasing awareness amongst behaviorists, ecologists, and game theorists that animals often operate in stochastic and indeterminate environments. Because of this, it is now widely agreed upon that animals often make decisions based on information that is incomplete, incorrect, or imperfect. The disciplines listed above all investigate different ways in which imperfect information affects biological systems. Behaviorists have two major interests that relate to this topic. The first involves the conventions of animal communication (Dawkins and Guilford, 1991; Hasson, 1994; Johnstone and Grafen, 1993; Krebs and Dawkins, 1984; Semple and McComb, 1996; Wilson, 1975). The second is sexual selection (Dale and Slagsvold, 1994; Funk and Tallamy, 2000; Getty, 1995, 1996; Searcy et al., 1991). Ecologists, on the other hand, are largely concerned with how imperfect information affects predator-prey relationships and foraging behavior (Abrams, 1994, 1995; Bouskila et al., 1995;

Luttbeg and Schmitz, 2000; Sih, 1992; Valone and Brown, 1989). Lastly, game theorists are beginning to become interested in how stochastic errors in social interactions may affect the evolution of social systems and "altruism" (Grim, 1995; Nowak, 1990; Nowak and Sigmund, 1992, 1993).

Because each of these disciplines has contributed to the understanding of how animals may interpret ambiguous (*i.e.,* noisy) systems that provide imperfect information, it is necessary to review some of the studies that each discipline has produced. Such a review will perhaps provide insight into how imperfect information is generated and the consequences that it can have. As implied above, there have been four major topics of study that have been particularly affected by the concept of imperfect information. They are as follows: (1) animal communication, (2) sexual selection, (3) game theory and the modeling of social evolution, and (4) predator-prey relationships and patch quality assessment.

LITERATURE REVIEW

Definitions

There is no universal agreement on many fundamental terms in the scientific literature. In particular, the terms communication, information, and signal are the main sources of confusion. Because some of the differences in the various definitions of these terms are due to more than just semantics, I shall compare and contrast some of the different ways that scientists conceptualize these terms.

Communication.---Wilson (1975) defined biological communication as "action on the part of one organism that alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants." While this definition leaves the nature of the modifying “action” open ended, the requirement that communication be “adaptive” probably places restraints on what is, or is not, communication. Hasson (1994) defined communication as “the transfer of a signal or signals from a signaler to (a) recipient(s)." At first glance, this appears to be a less restrictive definition of communication than Wilson’s definition. However, it relies on the term signal, which is a term with several definitions (see below). Moreover, the term signal is often defined with respect to the term information, which has been a source of debate in its own right.

Information.---Krebs and Dawkins (1984) made the distinction between “information theory” (*sensu* Shannon and Weaver; see Krebs and Dawkins, 1984, and Wilson, 1975, for reviews) and “semantic information.” According to Krebs and Dawkins (1984), information theory defines information as a “reduction in uncertainty of an observer about the actor’s or reactor’s behavior contingent upon a signal.” Conversely, semantic information is simply informative about "objects." For example, semantic information may contain information about an animal’s hunger state or overall physical condition.

There have also been attempts to define information in terms of its functional importance. Stephens (1989) defined information in terms of its value as follows: “the value of information is the difference between the expected payoff given that a different tactic can be chosen to match each state and the expected payoff given that a single tactic must be chosen to cover all possibilities.” Hasson (1994) preferred to view information in terms of how it changes the organism’s perception. Hasson stated “when perception of environmental parameters ultimately alters the probabilities of the organism’s actions, we recognize a change in its information." Thus, according to Hasson (1994), there are two types of changes in information. A positive change occurs when "the resultant choice of actions improves the individual's fitness." A negative change occurs when "the [resultant] choice of actions decreases the individual's fitness."

Signal.---Perhaps the most important thing to realize about the different definitions of the term signal is that some definitions are more restrictive than others. For example, Wilson (1975) defined a signal as "any behavior that conveys information from one individual to another." Conversely, Krebs and Dawkins (1984) advocated the notion that signals must be ritualized (*i.e.,* either exaggerated or repetitive in nature).

Hasson (1994) opted for a more involved concept of signals. He argued that when defining what a signal is, it is helpful to divide an individual's fitness into a social component (*e.g.,* interactions with other organisms regarding status and mating) known as the S-component and a non-social component (*e.g.,* based on ability to forage and escape predators) known as the F-component. According to Hasson (1994), signals must necessarily have a "non-positive" effect on the signaler's F-component. However, producing a signal can have either a positive or non-positive effect on the signaler's S-component depending on the situation (for example, a dominance display versus a submissive display). Hasson (1994) also distinguished between informative signals that improve a recipient's "choice of actions" and non-informative signals that "worsen the recipient's choice of actions."

Signal Honesty, Manipulation, and Deception

For some time, ethologists have debated whether signals between individuals are honest in terms of the information that they convey. The biggest proponent of signal honesty has been Zahavi. Zahavi (1975) originally argued for the evolutionary stability of signal honesty in a sexual selection framework. According to Zahavi's (1975, 1991) handicap principle, signals necessarily convey honest information because signals are costly, and less fit individuals cannot afford, or are physically incapable of, signaling as intensely or rigorously as more fit individuals. However, other authors (Dawkins and Guilford, 1991; Hasson, 1994; Johnstone and Grafen, 1993; Krebs and Dawkins, 1984; Semple and McComb, 1996) have disagreed with Zahavi's notion that signals are necessarily honest. For instance, Krebs and Dawkins (1984) argued that animal communication systems are most likely riddled with "exploitation" and "manipulation" because signals embodied with these qualities will often serve animals' own selfish interests (*sensu* Dawkins, 1989). Similarly, Dawkins and Guilford (1991) provided a strong argument for dishonest signaling. However, they based their argument on the notion that, in many communication systems, receivers will pay a price for assessing a signal. Because of this, when there are no harsh consequences for having incomplete information, receivers may only partially assess signals (*i.e.,* signals will become "conventional") (Dawkins and Guilford, 1991). When this occurs, communication systems are susceptible to low levels of cheating because information transfer is incomplete (Dawkins and Guilford, 1991; Semple and McComb, 1996).

Another mechanism by which deceptive signals can arise was put forward in a formal model by Johnstone and Grafen (1993). They argued that when there is phenotypic variation in a signal, there will always be "noise" in the communication system at the receiver's end (*i.e.,* there will be some error in the receiver's assessment of the signal). Johnstone and Grafen (1993) further argued that when such a "noise" exists, a system is left open to cheaters who may be capable of consistently using errors on the receiver's end to their own advantage. As a word of caution, it is important to note that the error rate of a system, due to variance in the phenotypic expression of a signal, does not constitute cheating (Dawkins and Guilford, 1991). A “noise” of this type only facilitates the evolution of cheaters.

Dishonest signals as a source of imperfect information.---Many ethologists seem to agree that low levels of deception and cheating are possible in stable communication systems. Obviously, when animals send out deceptive signals, they can cause receivers to experience negative changes in their information (*sensu* Hasson, 1994, see above). Furthermore, it is becoming increasingly clear that deceptive, manipulative, and cheating signals “alter the probability pattern of behavior” of the receiver and should therefore be considered communication, at least in the Wilsonian sense (see above).

The concept of imperfect information is becoming an integral part of studies on sexual selection. Several recent studies on sexual selection (see below) have supported the notion that dishonest signaling does take place in some systems. Furthermore, ideas stemming from studies on sexual selection, such as sensory bias (Ryan and Keddy-Hector, 1992), are helpful in understanding how dishonest and manipulative signaling can evolve. Because sexual selection has been the focus of most of the empirical studies that have evaluated how animals handle imperfect (*i.e.,* inaccurate or incomplete) information, I review some of these studies.

Sexual Selection and Mate Deception

One of the most documented cases of mate deception occurs in pied flycatchers (*Ficedula hypoleuca)* (Getty, 1995, 1996; Searcy et al., 1991; Svein and Slagsvold, 1994). Pied flycatchers represent a unique chance to study how animals handle imperfect information, in a sexual selection context, because of their breeding system. Male pied flycatchers often demonstrate polyterritoriality (*i.e.,* defense of two or more distinct territories) (Getty, 1995, 1996; Searcy et al., 1991; Svein and Slagsvold, 1994). It is not uncommon for the males of this species to pair with a female on one territory while actively displaying to different females in another territory (Searcy et al., 1991). Moreover, females occasionally choose mated males although when they do so, their offspring receive reduced paternal care.

One hypothesis that has been proposed to explain why female pied flycatchers occasionally pair with mated males is the deception hypothesis (Searcy et al., 1991; Svein and Slagsvold, 1994). According to the deception hypothesis, females pair with mated males because they are not aware of the males' breeding statuses. Searcy et al. (1991) found that mated males significantly altered their behavior patterns while in their secondary territories, when females were present, in a way that was likely to make their sexual statuses less clear to these females. However, Svein and Slagsvold (1994) concluded that females are probably able to counter some of the males' deceptive behaviors by visiting the males' secondary territories repeatedly and thus gaining information about how often these males are occupying these territories. Hence, the most likely scenario is that males attempt to deceive females with dishonest signals while females attempt to counter this tactic by repeatedly sampling male territories (Getty, 1995).

In the mating system of the pied flycatcher, it is likely that females are forced to make nesting decisions based on information that is likely to be conflicting (*i.e.,* imperfect information). For this reason, Getty (1995, 1996) advocated the use of signal detection theory (SDT) for analyzing this system. Essentially, SDT investigates the tradeoff between females "correctly" choosing an unmated male versus "incorrectly" choosing a mated male (Getty, 1996). Thus, SDT may be valuable to understanding how imperfect information affects the fitness of female pied flycatchers.

The problem of imperfect information, in a sexual selection context, is not restricted to vertebrates. Funk and Tallamy (2000) presented data that imply that deceptive behavior affects mate choice in long-tailed dance flies (*Rhamphomyia longicauda)*. This species is interesting because the two sexes have experienced roll reversal, so that females form leks from which the males choose their mating partners (Funk and Tallamy, 2000). A comparison between *R. longicauda* and a related species, *R. sociabilis,* implies that sensory bias (*sensu* Ryan and Keddy-Hector, 1992) may have facilitated the evolution of deceptive signaling in *R. longicauda* (Funk and Tallamy, 2000).

In *R. sociabilis,* abdomen diameter provides a reliable signal to males about the ripeness of a female's eggs. Thus, males of *R. sociabilis* prefer to mate with females that have abdomens that are large in diameter. Interestingly, males of *R. longicauda* also prefer females with larger abdomens. However, females of *R. longicauda* are capable of inflating "expandable pouches in the pleural margins of [their abdomens]" and, thus, superficially making their abdomens appear larger (Funk and Tallamy, 2000). Furthermore, females of *R. longicauda* can also increase the appearance of the size of their abdomens by encircling their inflated abdomens with their metathoracic legs (Funk and Tallamy, 2000). Thus Funk and Tallamy's findings suggest that females of *R.*

longicauda are capable of exploiting a sensory bias in males for large abdomen size in females. Because of this, it seems likely that male long-tail dance flies face the problem of erroneous (imperfect) information when deciding with which female to mate.

Game Theory and Social Evolution

The game known as the iterated prisoner's dilemma is one of the most commonly discussed and accepted models of social evolution available to behavioral ecologists (see Dawkins, 1989, for a detailed review of the prisoner's dilemma and reciprocity). In this game, two players have the option of either cooperating with each other or not cooperating with each other. The payoff matrix is denoted as follows: (1) If both players cooperate (C) they both receive R points, (2) If both players defect (*i.e.,* do not cooperate) (D) then both players receive P points, (3) If one player opts to cooperate but the other player defects (CD) then the defecting player (the exploiter) receives T points and the cooperating player (the exploited) receives S points. In order for the conditions of the iterated prisoner's dilemma to be met, the point matrix must be arranged so that $T > R > P > S$ and $2R > T + S$ (Nowak and Sigmund, 1993). Usually, tournaments have been held in which different human gamers submit different strategies that compete against one another in a computer simulated 'round robin' competition of the iterated prisoner's dilemma (iterated because there are repeat encounters between the same 'individuals'). Traditionally, these evolutionary models have assumed homogenous populations and error free interactions between 'individuals' (*i.e.,* individuals communicate in noise free systems) (Nowak and Sigmund, 1992). Under such conditions, a strategy known as "tit for tat" (TFT), in which an individual always initially cooperates and then subsequently mirrors its opponents previous move, has faired particularly well (Dawkins, 1989).

However, it has recently been shown that, as long as there is initially a small number of TFT-like strategies in the population, that an even more “generous” strategy is more evolutionarily stable than TFT if small stochastic error rates are programmed into the competing strategies (Nowak, 1990; Nowak and Sigmund, 1992). Nowak (1990) proposed that this is the case because errors between two TFT players can lead to a never ending “sequence” of “mutual” defection. Thus, it may pay “individuals” to be more forgiving when there is noise in a communication system. Grim (1995) found that the addition of a “spatial” component (attempting to simulate localized populations or kin groups) to the Nowak and Sigmund (1992, 1993) model further increased the degree of “generosity” that was stable.

Finally, it has been suggested that imperfect information may affect wars of attrition (Walton and Nolan, 1986). Walton and Nolan (1986), in their evaluation of pre-existing data on territorial disputes between male prairie warblers (*Dendroica discolor)*, concluded that these data were consistent with the hypothesis that disputes may become exceptionally prolonged because one or both of the contestants is operating on imperfect information. Walton and Nolan (1986) proposed that this may occur because, when prairie warblers arrive at their seasonal territories after spring migrations, it may be possible for one male to establish a territory in another male’s territory (according to Walton and Nolan, prairie warblers show site tenacity across seasons) without being aware that this has occurred. Consequently, one or both of the males may be confused about its territorial status (*i.e.,* resident versus intruder) (Walton and Nolan, 1986).

Although their conclusions must be considered tentative, because they were based on small sample sizes, Walton and Nolan (1986), at the very least, presented a plausible alternative hypothesis about why some territorial contests between male prairie warblers are unusually prolonged.

Predator-Prey Relationships and Patch Quality Assessment

Mathematical modeling.---Traditionally, when ecologists have modeled predator-prey relationships and foraging behavior, they have assumed that animals have perfect information. However, recently scientists have begun to realize that "assumptions about perfect information probably are not realistic" (Luttbeg and Schmitz, 2000). One idea that has received considerable attention is the possibility that animals face a tradeoff between the costs of obtaining information and operating on information that is imperfect (Abrams, 1994; Bouskila et al., 1995; Koops and Abrahams, 1998; Sih, 1992). In particular, this tradeoff has been viewed in the context of foragers who are uncertain about predation risk. This tradeoff leaves hypothetical foragers with two choices. They can either overestimate predation risk or underestimate predation risk.

Sih (1992) modeled a scenario in which animal prey had the choice between occupying unproductive, but safe, refuges or occupying productive, but dangerous, "open habitat." Sih's (1992) model predicted that it may often be beneficial for prey to remain in safe patches of habitat even when predators are not present in more productive areas (*i.e.,* overestimate predation risk) when uncertainty is sufficiently high. Similarly, models discussed by Bouskila et al. (1995) imply that animals are likely to overestimate predation risk if the cost of obtaining information is large enough to make their error rates of predation risk >40 %.

Abrams (1994) was skeptical of the generalized conclusion that animals usually overestimate predation risk. According to him, whether animals favor overestimation or underestimation of predation risk depends on which strategy results in behaviors that have lower “fitness cost[s].” Abrams (1994) contended that starvation rates may play a large role in what a given animal’s fitness costs are, relative to underestimation/overestimation, and that realistic starvation rates have a large enough range so that either strategy could be favored depending upon the organism.

One of the issues at the center of the debate over whether animals will overestimate or underestimate predation risk is how tolerant animals are to imperfect information (Koops and Abrahams, 1998). Generally, models that have favored overestimation have concluded that animals should be fairly tolerant of imperfect information because gaining more information only moderately increases their fitness (Bouskila et al., 1995; Koops and Abrahams, 1998). Conversely, Abrams (1994) argued that “there are few biological systems in which better information about effective predator density would have no effect on fitness.” Koops and Abrahams’ (1998) recent model has at least partially resolved this debate. They modeled how organisms, with different life histories, should differ in their tolerance to imperfect information and concluded that no generalizations “can be drawn concerning an expected observation of over- versus underestimation of predation risk.” However, Koops and Abrahams (1998) did conclude that “the greater the rate of increase in fitness with respect to increasing energy reserves, the more tolerant an animal should be to imperfect information.”

SYNOPSIS

The main purpose of this review is to establish that many biological systems that convey information have some noise that is inherent to the mechanisms by which they operate. Possible proximate causes of this noise include (1) conflicting needs of signalers and receivers (*i.e.,* signal dishonesty including manipulation, deception, and cheating), (2) organisms not being omniscient and consequently experiencing lag-times between updates on information that affects fitness (*e.g.,* estimates of predation risk), and (3) random errors in communication in which signals are either misrepresented or misinterpreted (*i.e.,* multiple phenotypes of a display and social evolution). All of these phenomena represent sources of imperfect information. Now that scientists are aware of imperfect information, it may be worth while to gather empirical data on how ambiguous information changes patterns of animal behavior.

Perhaps more than any other discipline, the field of animal behavior will benefit from a better understanding of how imperfect information affects communication systems and the patterns of both signaler and receiver behavior. Ethologists should attempt to work out the details of how imperfect information affects behavior patterns, so that this information can be applied to problems such as the ones reviewed above. In particular, a better understanding of this topic may increase the possibility for both foraging and game theoretic models to be made more realistic. Thus, the first step to better understanding the consequences of imperfect information in biological systems is largely ethological.

Chapter 2: *PLETHODON CINEREUS* AS A MODEL ORGANISM:

TERRITORIALITY, VISUAL DISPLAYS,

AND CHEMICAL COMMUNICATION

INTRODUCTION

A better understanding of how imperfect information alters animal behavior is likely to improve the scientific community's understanding of problems in several fields. Specifically, animal behaviorists, sociobiologists, and ecologists will benefit considerably from a better understanding of this topic. However, an increase in knowledge on this topic will require an understanding of how organisms handle information with little ambiguity (nearly perfect information) and then comparing the behavioral trends exhibited under these conditions with the behavioral trends exhibited when similar information is purposefully made imperfect. Thus, research of this nature can be approached in two different ways. The first, and more time consuming approach, is to pick an organism for which the social structure and communication processes are not well documented. The researcher could then determine these processes and monitor how behavior changes as information becomes more imperfect. The second, and more sensible, approach is to choose an organism for which the social structure and communication processes are already well documented and then investigate how behavioral patterns change as information becomes more imperfect.

The red-backed salamander (*Plethodon cinereus)* is an organism for which the communication, signaling, and behavioral patterns are well documented (see Jaeger, 1986, Jaeger and Forester, 1993, and Petranka, 1998, for reviews). Moreover, red-backed salamanders are small, easy to collect in large numbers, and well suited for laboratory studies where a large degree of control can be achieved. For these reasons, *P. cinereus* is likely to make an excellent model on which to study the affects of imperfect information on animal behavior.

RED-BACKED SALAMANDERS: NATURAL HISTORY, TERRITORIALITY, CHEMICAL COMMUNICATION, AND VISUAL DISPLAYS

Natural History of Plethodon cinereus

Plethodon cinereus is a relatively small terrestrial salamander that occupies much of the eastern part of North America (Petranka, 1998). Hatchlings appear much like miniature adults, and development to sexual maturity takes at least two years (Petranka, 1998). Like all plethodontid salamanders, *P. cinereus* has no lungs. Thus, respiration occurs across the skin. Hence, the maintenance of moist skin is essential to the survival of individuals of this species. Consequently, red-backed salamanders tend to become highly active during rainy periods. During these wet conditions *P. cinereus* will forage for invertebrate prey in the leaf litter of the forest floor (Gergits and Jaeger, 1990b; Jaeger, 1984). As water becomes a limiting factor, *P. cinereus* begins to seek out moisture under logs and rocks which also harbor prey. It is thought that because refuges are finite in number relative to the number of red-backed salamanders per patch of habitat (mean = 2.8 red-backed salamanders per square meter at my research site, Mathis, 1991b), this species has responded to these ecological pressures over evolutionary time with territorial behavior (see below).

Territoriality

Site tenacity.---Territoriality is well documented in *P. cinereus*, and there is evidence that this species possesses behavioral traits that are commonly associated with territorial species. First, *P. cinereus* exhibits site tenacity. It is not uncommon for this species to home to a cover object from over 30 m away (Jaeger et al., 1993). Furthermore, Gergits and Jaeger (1990a) demonstrated that *P. cinereus* often shows extreme site fidelity. In a repeated survey, Gergits and Jaeger (1990a) found that 91% (*n* = 90) of the animals that they sampled were found within 1 m of their original capture site.

Advertisement.---Next, *P. cinereus* actively advertises small territories under cover objects on the forest floor to conspecifics with chemicals. Laboratory experiments have shown that males of *P. cinereus* tended to be attracted to burrows marked with their own fecal matter and that they avoided the fecal matter of conspecifics (Jaeger et al., 1986). Similarly, Horne and Jaeger (1988) found that females of *P. cinereus* are "more passive toward their own fecal pellets than towards pellets of other females." Unfortunately, most of the data that indicate that red-backed salamanders advertise their territories with chemicals come from laboratory studies. Due to technical difficulties, little is known about territorial advertisement by *P. cinereus* in the forest (but see Gergits and Jaeger, 1990b).

Active defense and eviction of competitors.---Evidence for territorial defense in red-backed salamanders also comes from laboratory studies. Of particular importance is that agonistic encounters, including aggression, can be staged in the laboratory by allowing one animal to establish a "territory" and then introducing an intruder (da Silva Nunes and Jaeger, 1989; Horne, 1988; Lang and Jaeger, 2000; Thomas et al., 1989; Townsend et al., 1998). Experimental data suggest that agonistic behavior, in residents, increases with the amount of time that an individual occupies a territory (da Silva Nunes and Jaeger, 1989). There is also experimental evidence suggesting that asymmetries in length of territorial ownership may influence the outcome of territorial disputes in this species (Townsend et al., 1998). It has been hypothesized that a positive asymmetry in length of territorial ownership may "partially offset a negative asymmetry in body size" during territorial confrontations between red-backed salamanders (Townsend et al., 1998).

Chemical Communication

As mentioned above, red-backed salamanders use chemicals to advertise their territories (Horne and Jaeger, 1988; Jaeger et al., 1986). The literature also suggests that chemical signals are important to courtship and information transfer in *P. cinereus.* Gergits and Jaeger (1990b) described the courtship behavior of *P. cinereus* in a natural environment and suggested that males locate females via "pheromonal trails." Their description also suggests, albeit anecdotally, that the mental gland is a possible source of chemicals that may be important to the breeding process.

Some evidence implies that red-backed salamanders can uniquely identify individual conspecifics via olfactory reception of chemicals. McGavin (1978) found that red-backed salamanders nose tapped (chemodetection: see below) significantly more when presented with the chemical markings of a familiar conspecific than when presented with the markings of an unfamiliar conspecific. More recently, Gillette et al. (2000b) concluded that females of *P. cinereus* are capable of discriminating between familiar and unfamiliar male conspecifics "based on substrate cues alone."

Experimental studies have also indicated that *P. cinereus* may be able to obtain information on the state or condition of conspecifics by way of chemical cues. For example, Mathis (1990) found that intruders, in staged territorial conflicts, exhibited differential behavior patterns to secretions from individuals of different sex and body size. Moreover, Wise, Verret, and Jaeger (unpublished) collected data that suggest that red-backed salamanders can differentiate between the secretions of individuals with intact tails and individuals with autotomized tails. They suggested that this information may be valuable to red-backed salamanders who invade a conspecific's territory.

Possible sources of pheromone production.---Unlike many insects for which the chemical structures of many pheromones were deduced years ago (Wilson and Bossert, 1963), the chemical structures of the secretions used by *P. cinereus* are poorly known. What is more, the sites of production (presumably glands) of these chemicals are also poorly known. However, it is generally believed that the mental gland on the chin produces chemicals that are important to courtship (Simons and Felgenhauer, 1992). Behavioral observations and manipulations suggest that glands found in the proximal, ventral part of the tail (the postcloacal gland) may produce secretions that function as territorial markers (Jaeger and Gabor, 1993; Simons and Felgenhauer, 1992; Simons et al., 1994). Jaeger and Gabor (1993) found that "residents and intruders prefer to investigate... [the portion of the body] containing the postcloacal gland." Similarly, Simons et al. (1994) found that residents of *P. cinereus* directed lower levels of aggression towards conspecific intruders with "blocked" postcloacal glands than they did towards intruders whose postcloacal glands were functional.

Visual Displays and Observable Behavior Patterns

In addition to transfer of information via chemicals, *P. cinereus* also transmits signals via visual displays (Gabor and Jaeger, 1999; Jaeger, 1984; Jaeger and Forester, 1993; Jaeger and Schwarz, 1991). Such visual displays usually either convey threat or submission. Also of interest are the means by which red-backed salamanders investigate chemical odors (*i.e.,* nose tapping), direct aggression toward conspecifics, and exhibit escape behavior.

Threat posturing: all trunk raised.---Jaeger (1984) originally described and interpreted the all trunk raised (ATR) behavior pattern. The following is an excerpt from his original description: “All legs are extended downward such that the head and entire trunk are raised above the substrate, occasionally with the trunk arched. The tail may be entirely raised or distally resting on the substrate.” Jaeger (1984) hypothesized that ATR is a “look big” threat posture. Further research has suggested that ATR is a graded signal in which higher levels of threat are communicated by the extent of back arching and tail lifting (Jaeger and Forester, 1993; Jaeger and Schwarz, 1991; see Wilson, 1975, for a review of graded signaling).

Submissive posturing: flattened.---This behavioral pattern was initially described and interpreted by Jaeger (1984). One interesting aspect of the visual display system of *P. cinereus* is that the ATR posture and the flattened (FLAT) posture appear to exemplify the principle of the antithesis (Wilson, 1975). The following description of FLAT from Jaeger (1984) will make this clear: “The entire body is pressed against the substrate as in a submissive posture.” Thus, as Jaeger’s description implies, the general interpretation of FLAT is that it is equivalent to cowering.

Investigation of chemical odors: nose tapping.---Many plethodontid salamanders, such as *P. cinereus,* have nasolabial cirri that are believed to facilitate the transfer of odors to “chemoreceptors” in the nares (Dawley and Bass 1988, 1989). The behavioral response that is thought to correspond with this process is known as nose tapping (NT). Jaeger (1984) described NT in *P. cinereus* as the nasolabial cirri coming into contact with the substrate. Jaeger (1984) stated that NT could take place from either a resting posture (*i.e.,* front of trunk raised (FTR)) or ATR.

Aggression in red-backed salamanders: biting.---Biting in *P. cinereus* is a clear act of aggression. Jaeger (1981) observed that this species frequently directs bites at the areas of the snout, surrounding the nasolabial cirri and nasolabial grooves, and the tail. These foci of attack may represent body parts that, if damaged, cost a red-backed salamander in terms of future Darwinian fitness. Jaeger (1981) suggested that the area surrounding the nasolabial cirri and nasolabial grooves is often attacked because damage to the cirri or grooves may impair foraging abilities. Moreover, bites to the tail can result in the loss of this fat-storage appendage (Jaeger, 1981). Like attacks to the cirri, this may also decrease an individual's fitness because tail loss may confer an unfavorable asymmetry in body length upon an individual relative to the conspecifics with which it will be competing for territories (Wise and Jaeger, 1998).

Escape behavior in staged encounters.---This behavior is frequently observed in studies on this organism (Horne, 1988; Jaeger et al., 1982; Mathis, 1991a; Thomas et al., 1989; Wise and Jaeger, 1998). Escape behavior (EDGE) in *P. cinereus* consists of roaming around the edge of the arena as if trying to avoid an encounter with a conspecific (Horne, 1988; Jaeger et al., 2002; Mathis, 1991a; Thomas et al., 1989; Wise and Jaeger, 1998). If the encounters are staged in chambers (as they often are), red-backed salamanders may also push on the walls (Wise and Jaeger, 1998) or the lid (Horne, 1988; Thomas et al., 1989) of the container with their snouts. Thus, this behavior is usually interpreted as an attempt to flee an arena in which an encounter with a conspecific is staged.

SOCIAL MONOGAMY AND SEXUAL COERCION IN *PLETHODON CINEREUS*

Introduction

Recent laboratory studies (Gillette et al., 2000a; Jaeger et al., 2002) conducted on red-backed salamanders coupled with older field observations (Jaeger et al., 1995; Mathis, 1991b) have demonstrated that this species may have a mating system that is more complex than the mating systems of most amphibians. Mathis (1991b) showed that the territories of red-backed salamanders overlap more intersexually than intrasexually during the non-courtship summer. Moreover, Jaeger et al. (1995) found that out of 281 adult red-backed salamanders, 33% were found in male-female pairs under cover objects during the summer at the same site. These field observations prompted laboratory manipulations to investigate the possibility that social monogamy (Gillette et al., 2000a) and sexual coercion (Jaeger et al., 2002) are components of the red-backed salamander's mating system.

Social Monogamy

Gillette et al. (2000a) conducted a series of laboratory experiments to test the hypothesis that male-female pairs collected in the forest represent a subcomponent of the red-backed salamander's population that practice social monogamy *(i.e.,* that form relatively long term pair bonds). In total they carried out six different experimental scenarios: (1) a female, during the courtship season, was presented with a choice between the male with which she was found under a cover object in the field (*i.e.,* her "partner") and a novel male, (2) a male, during the courtship season, was presented with a choice between the female with which he was found under a cover object in the field (*i.e.,* his "partner") and a novel female, (3) a female, during the courtship season, was presented with a choice between a novel male, her "partner", and a surrogate, (4) a male, during the courtship season, was presented with a choice between a novel female, his "partner", and a surrogate, (5) a female, during the noncourtship season, was presented with a choice between her "partner" and a novel male, and (6) a male, during the noncourtship season, was presented with a choice between his "partner" and a novel female.

Gillette et al. (2000a) found that both male and female red-backed salamanders preferred to associate with their "partners" when their choice option was a conspecific of the opposite sex that was already "paired" (*i.e.,* that had been in association with a member of the opposite sex). However, both sexes showed no preference between their "partners" and "single" (unpaired) members of the opposite sex. Also, both males and females preferred their "partners" to surrogates, but neither showed a significant preference for surrogates versus a novel member of the opposite sex. Not surprisingly, during the noncourtship season, both male and female salamanders showed no preference between "partners" and novel members of the opposite sex.

Gillette et al. (2000a) suggested that these results could possibly be explained by red-backed salamanders having the ability to tell the "pairing status of a novel salamander based on the presence or absence of odors from other salamanders." These findings led Gillette et al. (2000a) to conclude that their results were consistent with the concept of social monogamy. Thus, they hypothesized that "free-living" salamanders "may form intersexual affiliations during the courtship season characteristic of social monogamy" (Gillette et al., 2000a).

Sexual Coercion

In laboratory experiments somewhat similar to those of Gillette et al. (2000a), Jaeger et al. (2002) tested the hypothesis that sexual intimidation (*sensu* Clutton-Brock and Parker, 1995) is a component of the red-backed salamanders' social system. In all, Jaeger et al. (2002) carried out four experimental treatments in both the breeding and nonbreeding seasons – yielding a total of eight treatments. Their treatments were as follows. (1) Socially polyandrous female "partners": a male had his "partner" removed from his presence (a chamber) and placed in a chamber with another male. The female was then returned to her original "partner" and the interaction between the two was observed. (2) Socially monogamous "partner": a male had his "partner" removed from his presence and placed in an empty chamber. The female was then returned to the male and their interaction was observed. (3) Socially naive female stranger: a male was introduced to a female that had no experience with other salamanders in the laboratory and their interaction was observed. (4) A female novel to the focal male, that had previously been in contact with another male, was introduced to the focal male, and their interaction was observed.

Jaeger et al. (2002) found that focal males did not behave differently in any of the treatments involving strangers (treatments 3 and 4 above) in either the courtship season or the noncourtship season. However, during the noncourtship season, Jaeger et al. (2002) found that males threatened socially polyandrous "partners" significantly more than they threatened socially monogamous "partners." Also, during the noncourtship season, males spent more time touching socially monogamous "partners" than they did touching socially polyandrous "partners." Finally, during the noncourtship season, males kept a greater distance between themselves and socially polyandrous "partners" than they did between themselves and socially monogamous "partners."

Jaeger et al. (2002) reported the following results during the courtship season of red-backed salamanders: (1) males displayed significantly more escape behavior when presented with a socially polyandrous "partner", (2) males kept a greater distance between themselves and socially polyandrous "partners" than they did between themselves and socially monogamous "partners", (3) males bit socially polyandrous partners significantly more than they bit socially monogamous partners, and (4) socially polyandrous females spent significantly more time in escape behavior than socially monogamous females.

From these results, Jaeger et al. (2002) concluded that sexual intimidation is more intense during the courtship season than it is during the noncourtship season. Similarly to Gillette et al. (2000a, see above), Jaeger et al. (2002) hypothesized that male red-backed salamanders are able to tell whether a female conspecific has been socially monogamous or polyandrous by whether her body carries the chemical cues of another male conspecific. Jaeger et al. (2002) stated that there was "no evidence that males mistook socially polyandrous females for intruding males because single males did not differ significantly in behavior towards intruding socially polyandrous and naive female strangers."

Chapter 3[1]: MULTIMODAL SIGNALS, IMPERFECT INFORMATION, AND IDENTIFICATION OF SEX IN RED-BACKED SALAMANDERS (*PLETHODON CINEREUS)*

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INTRODUCTION

Animal communication is often conceptualized as consisting of an animal that transmits a signal (the signaler) and another animal that receives the signal sent by the first animal (the receiver). Because receivers must ultimately process and interpret signals, what has become known as "receiver psychology" (Guilford and Dawkins, 1991; Rowe, 1999) has recently received theoretical and empirical consideration. In particular, three aspects of how the physical attributes of a signal interact with a receiver's "psychological landscape" (Guilford and Dawkins, 1991) have been of interest to researchers. (1) Detectability is how readily a signal can be perceived from background stimuli. (2) Memorability refers to "how easily a signal can be remembered, or associated with some other relevant stimulus" (Guilford and Dawkins, 1991). (3) Discriminability involves the categorizing of a stimulus into one "discrete" class versus another (Guilford and Dawkins, 1991).

Another idea that is important to studies of animal communication is the notion that animals often make decisions based on imperfect information (see Chapter 1): *i.e.,* information that is incomplete, incorrect, or misinterpreted. The concept of imperfect information has numerous applications to topics that are relevant to the study of animal behavior. Such topics include the modeling of predator-prey relationships and patch quality assessment (Abrams, 1994; Koops and Abrahams, 1998; Sih, 1992), game theoretic models of social evolution (Nowak, 1990; Nowak and Sigmund, 1992), and sexual selection (Funk and Tallamy, 2000; Getty, 1995, 1996; Searcy et al., 1991; Svein and Slagsvold, 1994).

There is an intuitive link between signal detection, memorability, and discrimination and imperfect information. For instance, if a signal is not detected, the intended receiver is likely to have incomplete or incorrect information about the signaler's intent, location of predators, or a host of other possible environmental parameters. Similarly, if a receiver has difficulty discriminating between two signals, then the receiver will likely misinterpret one signal for the other. Finally, if a receiver has difficulty remembering a signal, the receiver may have problems detecting the signal or remembering to which discrete class the signal belongs (*i.e.,* discriminating between the signal of interest and another similar signal).

Rowe (1999) concluded that multicomponent signals, and in particular multimodal signals (*i.e.,* signals that are in more than one sensory modality such as sight and smell), are generally easier to detect, remember, and discriminate than unicomponent and unimodal signals. There is a large amount of empirical support for Rowe's (1999) conclusions based on non-human subjects. For example, Hultsch et al. (1999) presented data demonstrating that oscine birds are better able to learn songs from recordings in the presence of a visual stimulus than when only the auditory stimulus is presented. Also, Hughes (1996) showed that the presence of both chemical signals and visual signals may increase a male big-clawed snapping shrimp's (*Alpheus heterochaelis*) ability to discriminate the sex of a conspecific. Rowe and Guilford (1999) demonstrated that the simultaneous presentation of particular olfactory and visual cues may be necessary for domestic chicks (*Gallus gallus*) to detect a warning signal *(i.e.,* neither vision nor smell presented alone elicited a response).

We used red-backed salamanders (*Plethodon cinereus*: Plethodontidae) to test the efficacy of multimodal signals in sexual discrimination. Red-backed salamanders are small terrestrial caudates that defend territories under rocks and logs in the forests of northeastern North America (Mathis, 1991b; Petranka, 1998). Territorial defense in *P. cinereus* may serve two functions: (1) to ensure access to invertebrate prey during dry periods (Jaeger, 1980) and (2) to ensure access to sites that are suitable for courtship, mating, and egg brooding (Mathis, 1991b).

Red-backed salamanders advertise and defend their territories via signals that occur primarily in two sensory modes. The first is olfaction. Jaeger et al. (1986) demonstrated that male red-back salamanders avoid burrows marked with the fecal matter of conspecifics but are attracted to burrows marked with their own fecal matter. Chemical signals in red-backed salamanders may also contain information about the status or condition of an individual. For example, McGavin (1978) and Gillette et al. (2000a) suggested that red-backed salamanders can discriminate between familiar and unfamiliar conspecifics solely from olfactory cues. Secondly, red-backed salamanders also transmit visual signals (Gabor and Jaeger, 1999; Jaeger, 1984; Jaeger and Forester, 1993; Jaeger and Schwarz, 1991). Of particular importance to territorial defense is the posture that is known as "all trunk raised" (ATR), which is associated with aggression (Jaeger, 1984).

Jaeger (1984) and Lang and Jaeger (2000) demonstrated that territorial male residents of *P. cinereus* are more aggressive toward male intruders than they are toward female intruders. This implies that males are capable of discriminating between males and females that enter their territories. Using *P. cinereus* as a model, we investigated the influence that imperfect information has on sexual discrimination of intruders by residents. We investigated this problem by making ambiguous the chemical information available to resident males about the sexual status of intruders (decreasing discriminability). In Experiment 1, resident males met male and female intruders that either were covered in secretions of the opposite sex (ambiguous signal) or were not covered in secretions of the opposite sex (unambiguous signal). These residents, then, had two signal modalities: olfactory and visual. Experiment 2 eliminated the visual signal by presenting resident male red-backed salamanders with swabs of female secretions, male secretions, and male and female secretions simultaneously. This experiment was conducted to see how behavior patterns change when the signal was reduced from a bimodal (visual and olfactory) signal to a unimodal (olfactory) signal.

METHODS

Collection

We collected 170 adult red-backed salamanders (100 males and 70 females) in Giles County, Virginia, USA in a section of Jefferson National Forest that is adjacent to Mountain Lake Biological Station (M.L.B.S.). We did not collect gravid females because visual information about their reproductive status may undermine attempts to "make" the sex of such animals ambiguous. Likewise, individuals of *P. cinereus* with autotomized tails were not collected because the behavior of residents differs depending on whether or not intruders have autotomized tails (Wise and Jaeger, 1998).

Processing, Storage, and Maintenance

Upon collection, each salamander was temporarily placed in a jar that contained paper towels moistened with spring water. They were then taken back to M.L.B.S. and sexed by checking for the presence of testes which can be seen through the abdomens of males (Gillette and Peterson, 2001). The salamanders were also measured for total length (TL) (length from tip of snout to tip of tail). No animals < 57 mm TL were kept (to insure that all animals were adults: Conant and Collins, 1998). Then, the salamanders were returned to their jars and transported to the University of Louisiana at Lafayette in a cooler that was packed with ice.

Once in the laboratory, the salamanders were placed in Petri dishes (14 x 1.5 cm) that were lined with coffee filters moistened with spring water. This lining was changed as needed and was moistened with spring water every two days. While in the laboratory, the salamanders were fed *Drosophila virilis* weekly and were kept on a 12L:12D light/dark cycle at 17 ± 2 degrees C.

General Protocol

Male salamanders were allowed to set up territories in experimental chambers (25 x 25 x 2 cm, Nune bioassay dishes: Cole-Parmer Co., Vernon Hills, Illinois) for five days prior to a trial, which is sufficient time for red-backed salamanders to establish territories (da Silva Nunes and Jaeger, 1989). We then subjected each male ($n = 30$) to three manipulations: (1) surrogate, (2) experimental (ambiguous), and (3) control (unambiguous). The order in which the male residents experienced these manipulations was randomized, and no focal animal experienced the same intruder (see below) more than once. In order to minimize any effects that stress, due to handling, may have had on resident and/or intruder behavior in Experiment 1, we placed both types of animals under a habituation dish for 15 min before data were recorded (da Silva Nunes and Jaeger, 1989). After this habituation period, the 15-min experimental trial began. During this trial, the following variables were measured: (1) time spent in the all-trunk raised (ATR) posture (threat: Jaeger, 1984), (2) time spent in front of trunk raised (FTR) (resting posture: Jaeger, 1984), (3) time spent in EDGE behavior (movement around the periphery of the arena while pushing against the roof or walls of the container as if trying to escape: Wise and Jaeger, 1998), (4) number of nose taps (reception of olfactory cues that involves touching the nasolabial cirri to the substrate: Dawley and Bass, 1988, 1989; Jaeger, 1984), (5) the amount of time that the resident spent TOUCHing the stimulus (*e.g.,* surrogate, experimental intruder or cotton swab, or control intruder or cotton swab), and (6) number of times that the residents bit the stimulus. For Experiment 1, these variables were also measured in the intruding animals to test whether or not differential behavior patterns by experimental versus control intruders influenced the behavior of focal males (*i.e.,* to increase our confidence that any significant results were indeed due to the olfactory manipulations). Both intruders (Experiment 1 only) and residents were fed on days 2 and 4 during the establishment period of a trial. Because morphological asymmetries can influence the outcome of territorial interactions between red-backed salamanders (Wise and Jaeger, 1998), we attempted to minimize such asymmetries between residents and intruders and between residents and source animals (see below) by keeping them within ±5 mm TL of one another.

Experiment 1: Live Intruder

Surrogate manipulation.---The surrogate manipulation consisted of presenting each resident male (n = 30) with a rolled up piece of paper towel, moistened with spring water, approximately the size of an adult *P. cinereus*.

Experimental manipulation (ambiguous).---The experimental manipulation consisted of presenting each resident male salamander (*n* = 30) with an intruder that had been swabbed with secretions from the opposite sex. There were two components to this manipulation: (1) the presentation of a female intruder swabbed with male secretions and (2) the presentation of a male intruder swabbed with female secretions.

The secretions used in such swabs were taken from source animals. These source animals were also used as intruders but a source animal for one resident was not used as an intruder for that same resident in any of the subsequent manipulations. We made swabs, all of which consisted of secretions from the following areas of the source animals' bodies: (1) underneath the chin, (2) the ventral part of the body, (3) the dorsal part of the body, and (4) the exterior surface surrounding the postcloacal gland, because these body parts are thought to contain glands that produce chemicals associated with territorial defense (Jaeger and Gabor, 1993; Simons and Felgenhauer, 1992; Simons et al., 1994). These secretions were obtained from source animals and applied to treatment intruders via a moistened (spring water) cotton ball.

Control manipulation (unambiguous).---The control manipulation consisted of presenting a resident male salamander (*n* = 30) with an intruder that had not been swabbed with secretions from the opposite sex. It consisted of two components: (1) a female intruder and (2) a male intruder.

Because the ambiguous manipulation consisted of handling the intruders in order to apply the secretions of the source animals, we attempted to neutralize stress due to handling in the control manipulation. Hence, control intruders were swabbed with cotton balls containing spring water prior to being presented to the residents. Three resident males escaped during experiment 1, which reduced our sample size to 27.

Experiment 2: No Intruder

This experiment consisted of the same design as Experiment 1 with the exception that cotton swabs containing the cutaneous secretions of red-backed salamanders, rather than live intruders, were presented to male residents (n = 30). The manipulations for this experiment were presentation of a cotton swab containing (1) spring water (surrogate), (2) secretions from a female, (3) secretions from a male, and (4) mixed secretions from both sexes (experimental manipulation, ambiguous). Each resident was tested once in each of the four treatments in random sequence. Behavioral response variables were as in Experiment 1.

Statistical Analyses

Resident data.---We tested whether or not the times that male residents spent in (1) ATR, (2) FTR, (3) EDGE, (4) TOUCH, and (5) number of nose taps differed among our manipulations via Friedman's analysis of variance by ranks for related data sets (Siegel and Castellan, 1988). This design and analysis may have two potential problems. (1) This design required calculating multiple Friedman's values (five for each experiment). Therefore, it is possible that some of our Friedman's values are significant due to chance. Because this research was largely exploratory in nature, we did not reduce alpha (as recommended by Jaeger and Halliday, 1998) because we considered it desirable to detect as many differences as possible in order to obtain the maximum amount of information available. (2) FTR and ATR cannot be exhibited by a salamander simultaneously. Hence, it is likely that these two variables are negatively correlated with one another. However, there is a third posture, which we do not report, known as FLAT (submissive: Jaeger, 1984) that may reduce the problem of autocorrelation between FTR and ATR. All Friedman's tests were deemed significant at $\alpha = 0.05$.

When differences were detected among the manipulations (via Friedman's ANOVA), the actual sources (*i.e.,* individual manipulations) of these differences were determined by sets of *a priori* contrasts that were calculated according to the algorithm put forth by Silverstein (1978). In Experiment 1, the following contrasts were determined *a priori* to be biologically relevant: (1) unambiguous female vs. surrogate, (2) unambiguous male vs. surrogate, (3) unambiguous male vs. unambiguous female, (4) ambiguous female vs. unambiguous female, and (5) ambiguous male vs. unambiguous male. In Experiment 2, the following contrasts were determined to be biologically relevant: (1) female secretions vs. surrogate, (2) male secretions vs. surrogate, (3) female secretions vs. male secretions, (4) female secretions vs. ambiguous secretions, and (5) male secretions vs. ambiguous secretions.

Intruder data (Experiment 1 only).---Because some intruders were used more than once in Experiment 1, the data are not entirely independent. However, because of the extremely large number of intruders that we would have needed to ensure independence (90 of each sex), we limited our collection for ethical and practical reasons. Thus, 31% of our intruder observations came from animals that were used twice, 14% from those used thrice, 4% from those used four times, and 51% from animals that were used once (n = 108). Because these data were analyzed to test the hypothesis that differences in resident behavior were not responses to differences in intruder behavior, we feel justified in using a statistical approach. Thus, we tested for differences in FTR, ATR, TOUCH, EDGE, and number of nose taps across manipulations using Kruskal-Wallis tests (Sokal and Rohlf, 1995). There were not enough instances of biting across the manipulations in either experiment to allow for statistical analyses. Thus, we only report in which manipulations biting occurred. Friedman's ANOVAs and Kruskal-Wallis tests were conducted on SPSS, Version 10.0 for Windows. *A priori* contrasts were calculated by hand (Silverstein, 1978).

Ethical Note

Bites by this species consist of a rapid nip with the anterior part of the mouth, which does not lacerate the skin of the bitten salamander, or a 'full mouth hold' which may lacerate the skin (Jaeger et al., 2002). We decided to intervene if a full mouth hold were to occur, but only nips occurred in our manipulations, so no intervention was necessary. We did not need to mark the salamanders for identification in Experiment 1 because the paired salamanders could be distinguished by unique color patterns. All salamanders were released near their site of capture following the experiments.

RESULTS

Experiment 1: Live Intruder

Intruder data.---Intruders did not behave significantly differently for any variable across the manipulations (Table 1). Intruders did not bite residents in any of the manipulations.

Table 1: Kruskal-Wallis values and descriptive statistics for intruder behavior from Experiment 1. Live intruders were UF = unambiguous female, UM = unambiguous male, AF = ambiguous female, and AM = ambiguous male.

Variable	Manipulation	*n*	Median (s)	Mean (s)	Range (s)	χ^2	df	*P*
FTR						1.51	3	0.680
	UF	27	429	452	843			
	UM	27	407	401	879			
	AF	27	279	383	823			
	AM	27	424	442	846			
ATR						7.30	3	0.063
	UF	27	72	101	462			
	UM	27	169	222	569			
	AF	27	46	132	621			
	AM	27	107	160	631			
TOUCH						1.76	3	0.625
	UF	27	27	58	227			
	UM	27	13	50	330			
	AF	27	24	56	561			
	AM	27	10	45	278			
EDGE						0.32	3	0.956
	UF	27	363	365	869			
	UM	27	381	352	748			
	AF	27	346	370	768			
	AM	27	359	341	846			
NT						0.02	3	0.999
	UF	27	4	8	23			
	UM	27	5	10	41			
	AF	27	5	10	49			
	AM	27	6	9	36			

Resident data.---Residents did not differ significantly in the amount of time that they spent in EDGE, nor did they differ in the number of times that they nose tapped (Table 2). There were significant differences across manipulations in the amount of time that residents spent in FTR, ATR, and TOUCH (Table 2). Biting occurred in the unambiguous male ($n = 2$), ambiguous female ($n = 1$), and ambiguous male ($n = 3$) manipulations.

A priori contrasts via Silverstein's (1978) technique for TOUCH yielded significant differences between the following pairs: unambiguous female > surrogate and unambiguous male > surrogate (Table 3). Post hoc analyses for FTR revealed significant differences between the following pairs: unambiguous male < surrogate, unambiguous male < unambiguous female, and unambiguous female > ambiguous female (cf. Tables 2 and 3). Likewise, contrasts for ATR yielded significant differences between the following pairs: unambiguous male > surrogate and unambiguous male > unambiguous female (cf. Tables 2 and 3)

Experiment 2: No Intruder

No significant differences occurred in resident behavior across manipulations for TOUCH, EDGE, and NT (Table 4). Significant differences were detected for FTR and ATR (Table 4). Biting did not occur in any of the manipulations.

Contrasts for FTR yielded significant differences for the following pairs: (1) female > surrogate, (2) male < female, and (3) ambiguous < female (cf. Tables 4 and 5). Contrasts for ATR revealed significant differences between the following pairs: (1) male > surrogate and (2) male > female (cf. Tables 4 and 5).

Table 2: Friedman's values and descriptive statistics for residents from Experiment 1: live intruder. UF = unambiguous female, UM = unambiguous male, AF = ambiguous female, and AM = ambiguous male.

Variable	Manipulation	*n*	Median (s)	Mean (s)	Range (s)	χ^2	df	*P*
FTR						25.13	4	<0.001
	Surrogate	27	690	615	753			
	UF	27	668	587	869			
	UM	27	293	358	839			
	AF	27	384	479	877			
	AM	27	310	368	857			
ATR						9.59	4	0.048
	Surrogate	27	42	68	318			
	UF	27	43	76	269			
	UM	27	113	259	836			
	AF	27	28	106	673			
	AM	27	68	121	498			
TOUCH						10.72	4	0.030
	Surrogate	27	0	13	137			
	UF	27	16	29	119			
	UM	27	6	31	181			
	AF	27	8	54	714			
	AM	27	19	36	297			
EDGE						3.01	4	0.542
	Surrogate	27	192	228	540			
	UF	27	166	248	824			
	UM	27	159	206	596			
	AF	27	262	286	818			
	AM	27	267	268	751			
NT						3.31	4	0.508
	Surrogate	27	6	10	40			
	UF	27	3	5	22			
	UM	27	3	5	20			
	AF	27	5	8	29			
	AM	27	5	7	25			

Table 3: *A priori* contrasts via Silverstein's (1978) technique for residents in Experiment 1: live intruder. Sur-UF = surrogate–unambiguous female, Sur–UM = surrogate-unambiguous male, UF–UM = unambiguous female–unambiguous male, UF–AF = unambiguous female–ambiguous female, and UM–AM = unambiguous male–ambiguous male. *n* = 27 for all tests. N.S. = not significant at the 0.05 level.

Variable	Pair	*Z*	*P*
FTR			
	Sur–UF	1.22	N.S.
	Sur–UM	5.36	<0.05
	UF–UM	4.14	<0.05
	UF–AF	2.79	<0.05
	UM–AM	0.16	N.S.
ATR			
	Sur–UF	0.56	N.S.
	Sur–UM	3.72	<0.05
	UF–UM	3.16	<0.05
	UF–AF	1.09	N.S.
	UM–AM	1.09	N.S.
TOUCH			
	Sur–UF	3.72	<0.05
	Sur–UM	2.69	<0.05
	UF–UM	1.01	N.S.
	UF–AF	0.23	N.S.
	UM–AM	0.56	N.S.

Table 4: Friedman's test values and descriptive statistics for resident behavior from Experiment 2: no intruder.

Variable	Manipulation	*n*	Median (s)	Mean (s)	Range (s)	χ^2	df	*P*
FTR						17.87	3	<0.001
	Surrogate	30	594	568	820			
	Female	30	754	661	848			
	Male	30	344	368	807			
	Ambiguous	30	272	355	900			
ATR						12.84	3	0.005
	Surrogate	30	19	35	129			
	Female	30	11	49	249			
	Male	30	136	289	839			
	Ambiguous	30	83	276	856			
TOUCH						0.87	3	0.831
	Surrogate	30	0	8	107			
	Female	30	0	11	220			
	Male	30	0	9	87			
	Ambiguous	30	0	12	163			
EDGE						3.91	3	0.271
	Surrogate	30	112	222	774			
	Female	30	108	196	624			
	Male	30	144	192	705			
	Ambiguous	30	219	263	763			
NT						6.98	3	0.073
	Surrogate	30	3	5	19			
	Female	30	6	10	63			
	Male	30	10	12	42			
	Ambiguous	30	6	11	67			

Table 5: *A priori* contrast results via Silverstein's (1978) algorithm for resident behavior in Experiment 2: no intruder. S–F = surrogate–female, S–M = surrogate-male, F–M = female–male, F–A = female–ambiguous, and M–A = male–ambiguous. *n* = 30 for all tests. N.S. = not significant at the 0.05 level.

Variable	Pair	*Z*	*P*
FTR			
	S–F	3.86	<0.05
	S–M	1.06	N.S
	F–M	4.92	<0.05
	F–A	5.30	<0.05
	M–A	0.38	N.S.
ATR			
	S-F	0.636	N.S.
	S–M	4.19	<0.05
	F–M	3.56	<0.05
	F–A	2.50	N.S.
	M–A	1.06	N.S.

DISCUSSION

Experiment 1: Live Intruder

Our analyses of intruder behavior imply that there is no reason to assume that residents behaved differently in response to differences in intruder behavior across manipulations. Male residents did respond in a statistically different manner to unambiguous female and unambiguous male intruders. In particular, resident males spent significantly less time in resting posture (FTR) and significantly more time giving threat displays (ATR) while facing unambiguous male intruders than while facing unambiguous female intruders. Our TOUCH data imply that male residents spent significantly more time touching both unambiguous male and unambiguous female intruders relative to the time they spent touching surrogates.

Experiment 2: No Intruder

Our data imply that resident males responded differently to the presentation of male and female chemicals in their territories. Resident males spent significantly more time in resting posture (FTR) and significantly less time in threat display (ATR) when presented with female secretions than when presented with male secretions. Interestingly, all the contrasts that we made for FTR were significant except for the male vs. ambiguous comparison and the surrogate vs. male comparison. For ATR, the surrogate vs. male and female vs. male contrasts were significant.

Sensory Modality and Ambiguous Situations

Our ability to detect consistent (*i.e.,* more time in FTR and less time in ATR in response to females vs. males) significant differences between how residents responded to males vs. females from the unambiguous manipulations of both experiments implies that either sensory modality (vision or olfaction) is sufficient for the correct identification of sex in unambiguous situations. Under ambiguous situations with both visual and olfactory cues present (Experiment 1), the male residents did not appear to be "confused" about how to allocate aggression (ATR). This result implies that vision is likely to be important to male residents of *P. cinereus* that are attempting to determine the sex of a conspecific. Hence, such residents may rely on morphological cues during the process of sexual identification.

Under ambiguous situations in which only olfactory cues were available to male residents, the residents spent less time resting (FTR) relative to when they were presented with female secretions. However, under the ambiguous manipulation of Experiment 2, male residents were intermediate, when compared with the male and female manipulations, in the amount of time that they spent in threat posture (ATR). These results have two implications. (1) Resident males may exhibit a heightened response (because they spend less time resting) when they are uncertain about the sex of an intruding conspecific. (2) Male residents may bet-hedge with respect to aggression (ATR) when they are uncertain of the sexual identity of an intruding conspecific. This type of response may be beneficial to resident males for two reasons. First, it may allow resident males to be alert and ready for an aggressive confrontation with an intruding male. Second, it may prevent resident males from being overly aggressive with an intruding female which could cause resident males to miss out on a potential mating opportunity.

In summary, our results imply that, when olfactory and visual information is available (Experiment 1), resident males "correctly" allocate aggression based on the sexual identity of the intruding conspecific in both unambiguous and ambiguous situations (*i.e.,* residents can discriminate between the sexes). When only olfactory information is available (Experiment 2), resident males appear to be able to detect the secretions of both sexes and discriminate between them so long as these signals are not made ambiguous. However, under ambiguous situations in which only olfactory information is available (Experiment 2), male residents appear to detect both components (male and female) of the signal, but discrimination does not take place.

We conclude that for male resident red-backed salamanders attempting to identify the sex of an intruding conspecific, that bimodal signals are not much more efficient than unimodal signals under unambiguous situations. However, as the quality of the information made available to male residents is reduced (*i.e.,* made ambiguous), bimodal signals appear to be superior to unimodal signals. Thus, for resident male red-backed salamanders attempting to determine the sex of an intruding conspecific, the amount of noise introduced to the signals that they receive may strongly influence how important sensory modality is to their success in making this determination.

Chapter 4: SUMMARY AND CONCLUSION

SUMMARY

This study is the first of which I am aware that specifically focuses on how intraspecific interactions between caudates change when the signals by which they communicate are made ambiguous. I conclude that the patterns of resident behavior observed in Experiment 1 were due to the experimental manipulations and were not responses to differences in intruder behavior. Experiments 1 and 2 both demonstrated that male resident red-backed salamanders responded differently to unambiguous males vs. unambiguous females and to male secretions vs. female secretions. The qualitative pattern of behavior that I observed in male residents was the same for both experiments (*i.e.*, increased time in FTR towards females and their secretions and decreased time in ATR towards females and their secretions).

In Experiment 1, male residents of *Plethodon cinereus* appeared to be able to identify correctly ambiguous males as male and ambiguous females as female despite receiving confounding olfactory information. In Experiment 2, resident males could not discriminate between male secretions and male and female secretions presented simultaneously. However, it appeared that male residents did detect both components (male and female) of the ambiguous manipulation of Experiment 2.

CONCLUSION

Bet Hedging and Ambiguous Scenarios

The results of this research may imply that resident males exhibit a heightened response when in ambiguous situations with respect to the sexual identity of an intruding conspecific. My data imply that male residents are more active when presented with ambiguous secretions but that they display aggression levels that are intermediate to the aggression levels that they exhibit when they are presented with male secretions and female secretions. This leads me to conclude that male residents may bet hedge with respect to aggression when they are uncertain of the sex of an intruding conspecific. Male residents may bet hedge when uncertain (with respect to the sex of an intruding conspecific) for two reasons. (1) Bet hedging may allow male residents to be "on guard" for an agonistic encounter with an intruding consexual. (2) Bet hedging may prevent resident males from being too aggressive with an intruding female which may keep resident males from missing potential mating opportunities.

Multicomponent Signals and Red-backed Salamanders

Although this research has focused on the relationship between sensory modality and receiver psychology, Rowe (1999) stated that multicomponent signals can occur within a single sensory mode. For example, visual signals that involve the movement of multiple body parts may be considered multicomponent signals. Similarly, olfactory signals that involve more than one chemical may be considered multicomponent signals. The problem that arises with multicomponent signals in a single sensory mode is that the different components may not be perceived as distinct (Rowe, 1999). Conversely, signals that have components distributed across different sensory modes are "more readily dissociated into their components" (Rowe, 1999). Hence, it is often convenient to equate different sensory modes with different signal components because it can make the determination of what a component is less subjective. However, while such categorization may be convenient for researchers, it is not necessarily reflective of what animal receivers perceive as a distinct signal component.

In red-backed salamanders, it is possible that both the visual and olfactory components of the signals that I studied are multicomponent signals in and of themselves. Support for this claim comes from Jaeger and Schwarz (1991) who demonstrated that ATR (threat posture) is a graded signal that involves the movement of multiple body parts in a particular sequence of events. Furthermore, it is possible that olfactory communication in *P. cinereus* consists of multicomponent signals that are made up of more than one chemical; however, this has not been documented.

For these reasons, it is important to note that, while my data do not support Rowe's (1999) claim that signalers will "benefit more consistently from producing components in multiple modalities rather than just one", they are not inconsistent with the overall theme of Rowe's (1999) review. Her theme was that multicomponent signals are easier to detect, discriminate, and remember than unicomponent signals. In the communication system of red-backed salamanders, it may not be safe to assume that the reduction from bimodal signal (vision and olfaction) to unimodal signal (olfaction) is equivalent to the reduction from a signal with two components to a signal with one component. Because of this, my inferences are limited to sensory modality and do not include statements about signal components.

OTHER THOUGHTS AND FUTURE STUDIES

Because red-backed salamanders in the natural habitat are thought to use chemical secretions in territorial advertisement (Horne and Jaeger, 1988; Jaeger et al., 1986) and because intersexual pairing may not be uncommon in this species (Gillette et al., 2000), there are potentially numerous scenarios in which red-backed salamanders could come into contact with male and female secretions simultaneously in the visual absence of any conspecifics. When this is considered in conjunction with Mathis' (1991b) hypothesis that there are a large number of 'floaters' in the population of *P. cinereus* that do not hold territories, the probability of a red-backed salamander encountering both male and female secretions simultaneously in the visual absence of a conspecific may be high. For instance, floaters that are passing through the territories of conspecifics may benefit from avoiding agonistic encounters with these territory holders. One potential way that this could be achieved is by floaters being sensitive to olfactory markings that indicate which territories (*i.e.,* territories held by males or by a male-female pair) are more likely to be treacherous.

A future line of study that may be informative would be to investigate how red-backed salamanders that are intruding on the territory of a conspecific behave when presented with a stimulus that is ambiguous with respect to sex. Such an experiment may be more ecologically relevant than the one presented above and could also potentially provide insight into the floater portion of the red-backed salamander population at Mountain Lake Biological Station. To my knowledge, information on this portion of this red-backed salamander population is scarce. Nevertheless, it is needed because the floating portion of the population is thought to be considerable.

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Page, Robert B. Bachelor of Science, Piedmont College, Spring 2001; Master of Science,
University of Louisiana at Lafayette, Spring 2003
Major: Biology
Title of Thesis: Signal Ambiguity and the Assessing of Imperfect Information in Red-backed Salamanders (*Plethodon cinereus*)
Thesis Director: Dr. Robert G. Jaeger
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ABSTRACT

Using the red-backed salamander, *Plethodon cinereus*, as a model, I investigated how male territorial residents' behavioral patterns changed or did not change when they were presented with social situations that were unambiguous vs. ambiguous. I did this by conducting two laboratory experiments. In the first experiment, I presented resident males with conspecific intruders that were (1) not manipulated in any way and (2) covered with the cutaneous secretions of a member of the opposite sex. A surrogate was also presented to resident males in this experiment to serve as a control. In the second experiment, resident males were exposed to (1) a surrogate, (2) female secretions, (3) male secretions, and (4) both male and female secretions simultaneously.

The results of Experiment 1 implied that male residents were not "confused" by the presentation of male intruders covered in female secretions or by the presentation of female intruders covered in male secretions. In Experiment 1, resident males behaved significantly more aggressively towards male intruders than they did towards female intruders and they spent significantly more time resting in the presence of female intruders than in the presence of male intruders. Resident males spent significantly more

time touching unambiguous male and unambiguous female intruders than they did touching surrogates.

Experiment 2 revealed the same overall patterns of male residents' behavior as in Experiment 1. In particular, male residents behaved significantly more aggressively and spent less time resting in the presence of male secretions than in the presence of female secretions. Resident males also showed intermediate aggression levels to the simultaneous presentation of male and female secretions relative to the presentation of male and female secretions separately (*i.e.,* male secretions > ambiguous secretions > female secretions).

BIOGRAPHICAL SKETCH

Robert Bryce Page was born on 19 October 1976 in Athens, Georgia. Robert grew up in Athens and graduated from Cedar Shoals High School in 1995. Robert then spent the next couple of years working at odd jobs and playing guitar in a number of obscure blues-based rock-and-roll bands. In 1997, Robert began attending college, and in May of 2001 he earned a Bachelor of Science degree in biology from Piedmont College. In August of 2001, Robert enrolled as a master's student at the University of Louisiana at Lafayette and in spring 2003 defended his thesis.