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## **The Effects of Social Experience on Aggressive Behavior in the Green Anole Lizard (*Anolis carolinensis*)**

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### **Abstract**

To understand how context-specific aggression emerges from past experience, we examined how consecutive aggressive encounters influence aggressive behavior and stress responses of male green anole lizards (*Anolis carolinensis*). Animals were shown a video clip featuring an aggressively displaying conspecific male, which provoked aggressive responding, while control animals viewed a neutral video. After 5 d of interaction with the videos, both the subject and control groups were presented with a live conspecific. As a non-invasive assay of stress responses, we measured changes in body color and eyespot darkness, two features known to be strongly correlated with titers of stress hormones. Our results demonstrate that experience increased aggression in male anoles, but that increases in aggression to a repeated stimulus were transient. Tests with a novel conspecific indicate that the experienced animals remained aggressive when presented with novel stimuli. Although there were differences in the morphological indicators of the stress response between experimental and control groups during video presentations, there were no differences when presented with novel conspecifics. These data indicate that experience-dependent differences were not mediated by differences in the ‘stressfulness’ of aggressive interaction, as thought to be the case for animals in chronic subordinate/dominant dyads. We suggest that habituation and reinforcement interact to promote aggressive responding and to restrict it to novel individuals. Such context specificity is a hallmark of natural patterns of aggression in territorial species.

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## Introduction

For many animals, successful reproduction centers on the ability to acquire and maintain a territory. Not surprisingly, the appropriate expression of territorial aggression requires a complex balance of variables: physiology (e.g. circulating levels of sex steroid hormones, Adkins & Schlesinger 1979; Wingfield 1985; Denardo & Licht 1993; Denardo & Sinervo 1994), physical capacity of an animal (indicated by body size, Tokarz 1985), and environmental conditions (e.g. population density, Wagner 1989; Brenowitz & Rose 1994; Stamps & Krishnan 1995, 1998; Burmeister et al. 1999; and territory quality, Leuck 1995). Different combinations of these factors may determine whether conspecifics will engage in territorial aggression in a given dyad, and the contribution of each component may differ from context to context. Moreover, the prior experience of an individual, such as the number of prior fights and familiarity with an area, has been shown to play a critical role in territorial aggression (see Crews 1974; Sapolsky 1993; Brenowitz & Rose 1994; Stamps & Krishnan 1994a, 1995, 1998). For example, the social history of an animal, such as whether it has previously been dominant or subordinate in a social hierarchy, influences the probability of winning subsequent fights (Greenberg et al. 1984; Stamps & Krishnan 1994a).

Many ethologists, particularly behavioral ecologists and life-history biologists, have examined trade-offs made to accommodate conflicting demands on territorial behavior and have reported that beneath such decisions lie proximate mechanisms that balance conflicting concerns and restrict aggression to appropriate contexts (e.g. Ketterson & Nolan 1992). The perceptual processes that underlie ecological decision making are receiving renewed attention (Real 1994; Hauser 1996; Dukas 1998), but many basic aspects of territorial aggression remain unexplored. In this study we examine how context-specific aggression emerges from controlled manipulations of aggressive experience.

Territory acquisition, indeed any history of winning fights, is often correlated with an increase in aggressiveness (reviewed in Stamps & Krishnan 1998). From an ultimate perspective, prior aggressive experience can be seen as a cue to the aggressor's fighting ability (although there are other reasons for territorial experience to facilitate aggression, e.g. see review in Krebs & Davies 1993; Stamps 1995). Once a territory is occupied and its boundaries established, residents ought to remain highly aggressive to novel intruders, but ought not to expend resources and risk predation or injury by fighting with well known neighbors – a phenomenon known as the 'dear enemy' effect (Fisher 1954).

The ability of prior experience to alter aggression and the ability to direct that aggression to strangers are both widely documented, but little attempt has been made to reconcile the two processes or to see how a single species implements both. We propose that habituation counters the influence of prior experience with particular individuals, enabling the appropriate context-specific expression of aggression. We tested this hypothesis by using video clips to manipulate the aggressive experience of territorial male green anoles, *Anolis carolinensis*. We

determined whether successful experience promotes aggression, whether repeated exposure to the same stimulus produces habituation, and whether this habituation is unique to the stimulus encountered.

We used *Anolis carolinensis* as a model system because the species shows a set of distinct and well-documented aggressive display behaviors that are easily quantified (Greenberg & Noble 1944; Crews 1975; Greenberg 1977; Greenberg & Crews 1990). Its three most conspicuous aggressive displays are the dewlap extension, push-up display, and lateral compression. Dewlap extension (DL) is a brief exposure of a conspicuous red throat fan that is normally retracted. Push-up display (PU) is a vertical movement of the front portion of the body. Both of these displays have been described as assertion displays (or 'male-alone displays', Decourcy & Jenssen 1994), which occur in response to a broad range of perturbations, including aggression (Greenberg & Crews 1990). Lateral compression (LC) is a sustained extension of the throat with sagittal expansion of the body, which makes the profile of the lizard appear much larger; it is considered a challenging or threatening (or 'male-male', Decourcy & Jenssen 1994) display toward an intruding conspecific (Crews 1975; Greenberg & Crews 1990). Unlike DL and PU, LC is unique to aggressive encounters.

To manipulate the experience of male green anoles with consecutive aggressive encounters, we exposed the anoles to a video clip featuring a conspecific male directing all three of these behaviors at the video camera. The use of video clips to simulate aggressive intrusion has been demonstrated to be as effective as the use of live conspecifics in field (Clark et al. 1997) and in laboratory settings (Macedonia & Stamps 1994; Macedonia et al. 1994). It also permits us to standardize the stimulus for all subjects.

Behavioral changes in aggressiveness are often accompanied by changes in the 'stressfulness' of aggressive challenges (Silverin 1993; Astheimer et al. 2000). To non-invasively assess whether changes in aggressiveness could be explained by differences in the stress response, we tracked changes in body color (BC) and the postorbital eyespot (ES) over the course of the study. It has been well documented that hormonal responses to acute and chronic stress are signaled by changes in BC and ES in *A. carolinensis* (Kleinholz 1938; Hadley & Goldman 1969; for a review, see Greenberg & Crews 1983, 1990; Greenberg et al. 1984; Summers & Greenberg 1994). Dark body color is associated with increased circulating melanotropin (MSH) and adrenal hormones in response to stress (Greenberg & Crews 1983, 1990; Greenberg et al. 1984). The body color of subordinate anoles after an aggressive encounter is darker than that of dominants (Greenberg & Crews 1990), and the dark body color of subordinates coincides with elevated circulating corticosterone (Greenberg et al. 1984). The dark coloration of ES reflects increases in circulating levels of catecholamine (Hadley & Goldman 1969; for a review, see Greenberg & Crews 1983, 1990) and has been widely used as an indicator of acute stress responses in this species (Summers & Greenberg 1994).

This procedure allowed us to examine how behavioral and physiological responses change with experience and, in both cases, how aggressive interactions

with a familiar opponent in a familiar context influence responses to a new challenger. If past success and habituation interact to permit the context-specific expression of aggression, we expect that repeated exposure to the video-taped male will lead to a transient increase in aggressive responding, followed by a loss of aggression directed at the video as the stimulus becomes familiar. If this habituation is specific to the video stimulus condition, exposure to a novel intruder should restore aggressive responding. Control animals who are exposed to a video without a displaying conspecific should show lower levels of overall aggression, and because they lack prior experience, should be significantly less aggressive in response to novel males. Habituation should make exposure to the aggressive stimulus less stressful. If the context-specific display of aggression is mediated independently of the stress response, as indicated by changes in colorations, there should be no differences between groups in the 'stressfulness' of a novel encounter. If, however, the acquisition of context-specific aggression is mediated by changes in the 'stressfulness' of encountering particular individuals, we expect changes in aggressive responding to be strongly correlated with our morphological indicators of stress during encounters with either familiar or novel males.

## Methods

### Animals and Materials

Adult male and female *A. carolinensis* were obtained from Bio Rep, Inc., La Place, Louisiana. The males' snout-to-vent lengths (SVL) ranged from 58 mm to 63 mm, a size range previously shown to include only sexually mature males. We housed conspecific females with each male in a clear glass cage measuring  $7 \times 12 \times 18$  inches on a 14-h light/10-h dark cycle for 2 wks prior to the experiment in order to maximize their aggressive responsiveness. Mating behavior between each couple was frequently observed throughout this housing period. Heat was provided by a 60-W lamp, and the room temperature was set at 32°C during the day and 22°C at night. The bottoms of cages were covered with sphagnum moss, and each cage contained a wooden diagonal perch. Water was supplied in gravel-filled water dishes, and crickets or mealworms were provided three times a week.

### Stimuli

Staged aggressive displays were recorded using a Panasonic AG-450 color video camera and Ampex S-VHS 120 videotape of a single session in which a medium ( $\approx 60$  mm) stimulus animal, implanted with a testosterone-filled silastic capsule, confronts a second animal of similar size. The session was recorded in an aquarium that was illuminated with two 60-W bulbs and whose back wall was covered with beige paper to eliminate reflection. The aquarium contained a

perch from which the videotaped stimulus male displayed to a second animal off camera. The video was recorded so that the apparent size of stimulus animal on the monitor screen would be the same as the size of an actual animal seen from the distance of the screen. Multiple 10-min video recordings were made until the video clip contained images of the stimulus animal showing all three types of displays (DL, PU, and LC) in two bouts within a 10-min period, whilst oriented towards the video camera. We used that final 10-min video clip for the experiment. The video playback ended with the stimulus animal jumping off the perch and out of sight. For video playbacks, we used a color video monitor (Panasonic CT-1384Y) and video cassette recorder (Panasonic PV-4311).

A control video was made showing two green balls (dimensions 4189 mm<sup>3</sup>) moving on the perch in the position occupied by a male in the standard video. The size of the image of the balls on the video monitor approximately matched the size of the stimulus male anole in the aggressive stimulus video. The balls were made to move at the same times and the ball motions were sustained for equivalent periods to the animal in the aggressive stimulus video clip. Thus, the two video clips were different only with respect to the stimulus objects shown. Similar methods have been used successfully in mate choice video playback experiments (Macedonia & Stamps 1994; Macedonia et al. 1994).

### Procedure

#### *Five-day exposure to video (video playback)*

We randomly assigned male *A. carolinensis* to one of two groups: aggressive video group (n = 9) and control video group (n = 9). SVL was not different between groups (ANOVA:  $F_{1,15} = 2.339$ , ns). Video presentation occurred whilst animals remained in their home cages to minimize any disturbance caused by the experiment. Animals in the aggression video group were exposed to the aggressive stimulus video once daily for 5 consecutive days. Animals in the control group were exposed to the control video clip on the same schedule. During the video playback, the room was darkened and only cage lights were on. Before each video session began, we double-checked that animals were looking at the video monitor. In each exposure trial, three distinct display behaviors and two color change measures of the subject animals (discussed in detail below) were measured by two experimenters.

#### *Test with a live conspecific male (test)*

One day after the last video playback, we presented each male with a conspecific male in an adjacent cage. Animals could interact with each other, but could not contact each other physically. One anole in the control group looked sick on the test day and was dropped from the study. The same behavioral and

color measures of both subject and stimulus animals were measured by two experimenters. As in the exposure trials, the room was darkened and only cage lights were on.

### Dependent Variables

We measured three types of aggressive displays (DL, PU, and LC). LC is the highest level of aggressive display behavior measured in this study. We counted the number of DL and PU that occurred during each trial. LC was considered a categorical variable, because whenever an animal showed an LC response, it usually lasted for a substantial length of time during a trial, so that any LC occurrence or non-occurrence within a given trial would be considered a 1 or zero, respectively. In addition, for coloration changes, BC was graded 1 through 5 as follows: light green (= 1), green with brown speckling (= 2), light brown or midway between green and brown (= 3), brown with some light speckling (= 4), and dark brown (= 5). The ES was graded from light green to black with a respective score from 1 (green) to 3 (black). For both BC and ES, higher numbers reflect greater stress. We measured changes in overall body color and changes in ES by subtracting the final scores from the initial scores.

### Statistical Analysis

Before analyses, DL and PU data were square-root transformed because their distributions were not normally distributed and positively skewed. Because DL and PU are highly correlated with each other (Pearson's correlation coefficient:  $r = 0.94$ ,  $p < 0.01$  for the video playback trials, and  $r = 0.93$ ,  $p < 0.01$  for the test), repeated measures of multivariate analysis of variance (repeated measures MANOVA) were performed for DL and PU with five video playback trials as a within-subject variable and video stimulus as a between-subject variable. Given both significant group differences in MANOVA, a repeated measures ANOVA for both DL and PU followed. The same statistical analysis was performed for changes in the two colorations. Lastly, post hoc Tukey tests were performed to test differences in each video playback trial.

To test group differences in the categorical measure, LC, over the five video playback trials, we counted the number of video playback trials in which a subject animal displayed LC out of a total of five video playbacks. A Mann-Whitney U-test was then performed. Upon finding a significant group difference in LC, a Pearson  $\chi^2$ -test within each video playback trial was performed.

For the test with a live conspecific, a MANOVA was performed with DL and PU displays as dependent variables followed by ANOVAs. The same analyses were performed for BC and ES measures. Differences in LC were tested with a Pearson  $\chi^2$ -test. All analyses were carried out by using the Statistical Package for Social Sciences (SPSS, Chicago, IL).

## Results

### Aggressive Responses in the Video Playback

The aggressive video playback group was significantly different from the control group in DL and PU (MANOVA:  $F_{1,15} = 6.13$ ,  $p < 0.03$ ) during the video playbacks (Fig. 1a, b). Subsequent ANOVA revealed that anoles exposed to the aggression video showed more PU than anoles exposed to the control video (ANOVA:  $F_{1,15} = 7.78$ ,  $p < 0.02$ ). Lastly, post hoc Tukey tests revealed that the aggression video group showed more DL than the control group in video playback Trial 1 ( $p < 0.05$ ) and showed more PU than the control group in video playback Trial 3 ( $p < 0.05$ ). Anoles in the aggression video group showed significantly more LC than control group animals over the 5-d video playback trials (Fig. 1c; Mann–Whitney U:  $z = -3.04$ ,  $p < 0.01$ ). Specifically, the aggression video group showed more LC in playback Trial 3 ( $\chi^2_1 = 6.30$ ,  $p < 0.01$ ), and a marginally significant group difference in LC was found in Trial 1 ( $\chi^2_1 = 3.24$ ,  $p < 0.07$ ). No LC was observed in the control group in any of the video playback trials. At the last playback trial on day 5, the aggressive video and control groups were not different, and both showed little aggressive response to the stimulus.

### Aggressive Responses in the Test

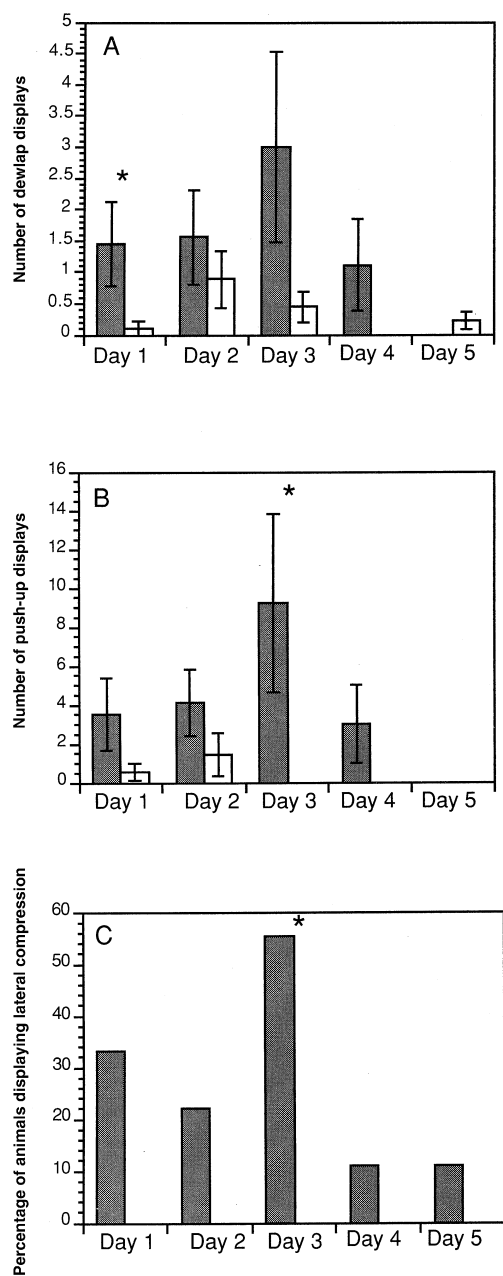
During the exposure to a live stimulus animal, the aggression video group showed significantly higher DL and PU (MANOVA:  $F_{2,14} = 6.96$ ,  $p < 0.008$ ). Specifically, these animals showed more PU ( $F_{1,15} = 9.32$ ,  $p < 0.008$ ) and more LC ( $\chi^2_1 = 7.14$ ,  $p < 0.008$ ) than the control group (Fig. 2).

### Changes in Colorations During the Video Playback

Anoles in the aggression video group changed their body color and ES to dark brown significantly more than the control video group during video playbacks (MANOVA:  $F_{1,15} = 6.72$ ,  $p < 0.02$ ; BC:  $F_{1,15} = 5.413$ ,  $p < 0.03$ ; and ES:  $F_{1,15} = 6.55$ ,  $p < 0.02$ ). Specifically, there was a group difference in video playback Trial 3 (BC:  $p < 0.05$ ; and ES:  $p < 0.01$ ; Fig. 3a, b).

### Changes in Coloration During the Test with Live Stimulus Animal

Both groups changed BC and ES into dark brown to the same extent during the test (MANOVA:  $F_{2,14} = 0.86$ , ns, Fig. 3c). In contrast to the behavioral results showing a higher aggressive response level in the aggression video group than that in the control group during the test, both groups showed equally high stress responses during the encounter with a live conspecific.



*Fig. 1:* Aggressive displays over the 5 d of video playbacks. The aggression video group (■) shows significantly more aggression over the trials than the control group (□) (overall  $p < 0.03$ ). Rates (means  $\pm$  SE) of dewlap extension (A) and push-up display (B) of both groups are shown. The percentages of animals displaying lateral compression during 5 d of video playbacks are also shown (C). No LC was observed in the control group. \*Indicates  $p < 0.05$  for individual day comparisons between groups



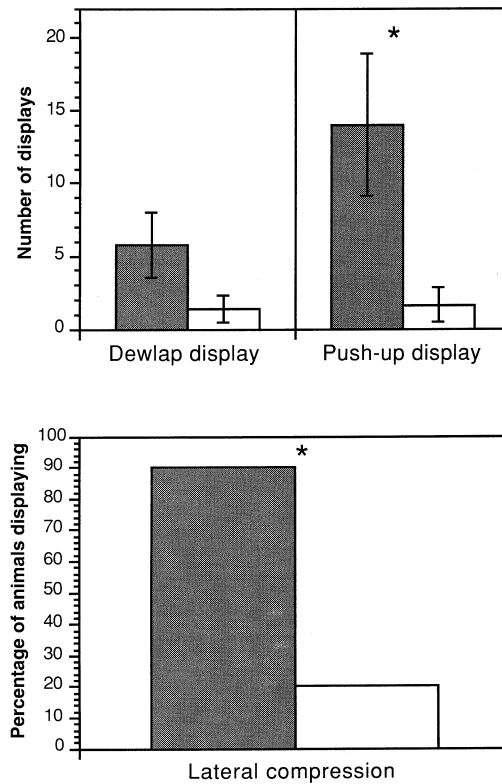


Fig. 2: Aggressive displays during exposure to a live stimulus animal. Aggression video group (■) shows significantly more aggression than control group (□). Rates (means  $\pm$  SE) of dewlap extension and push-up display during the test are shown in the top panel. The percentages of animals displaying lateral compression during the test are shown in the bottom panel. \*Indicates  $p < 0.05$  for individual comparisons

## Discussion

Our results demonstrate a biphasic change in aggressive behavior based on past experience. The ascending phase, in which prior experience potentiates further aggression, is evident in the early exposures to the aggressive video. However, the potentiating effects of experience seem to become latent during the last two video exposures. This apparent habituation is specific to the stimulus video condition, which includes both a specific individual and video stimuli, because presentation with a novel conspecific restores aggressive responding. We do not know what aspect of the video condition was responsible for the habituation. Those animals with prior experience against the stimulus video showed enhanced responses to novel males, indicating that the animals were able to generalize from video exposure to contests with other males.

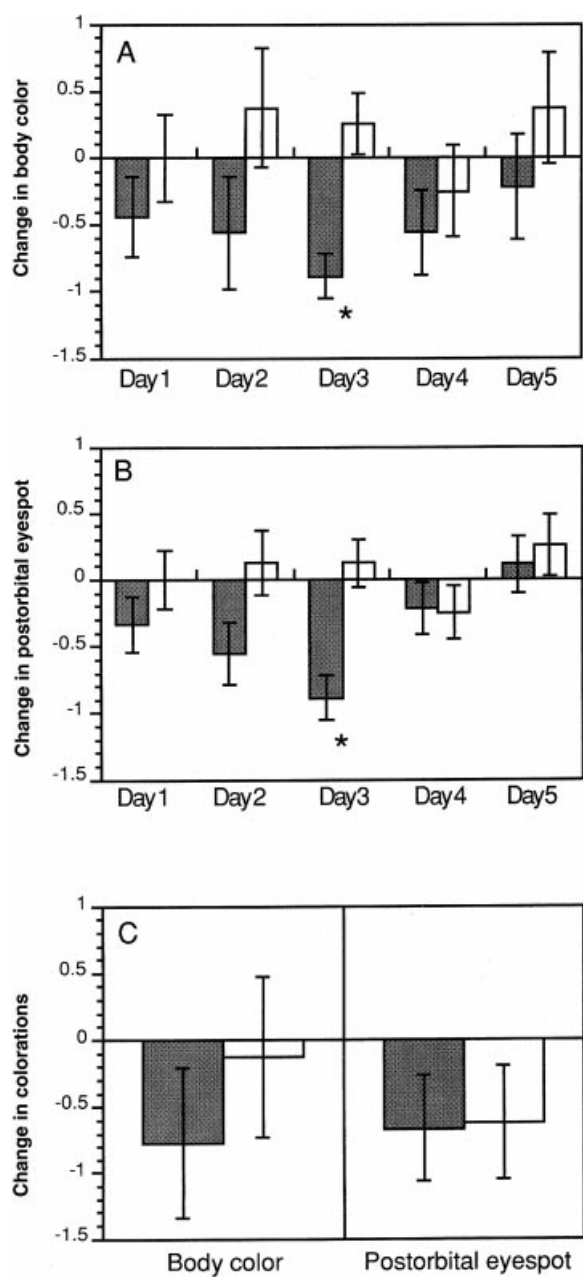


Fig. 3: Changes (means  $\pm$  SE) in body color and ES are depicted over 5 d of video playbacks (A, B) and test with a live stimulus animal (C) in the aggression video (■) and the control (□) groups of green anole lizards. Negative values in the y-axis indicate changes to brown, which suggests more stress. \*Indicates  $p < 0.05$  for individual comparisons

Our results agree with two apparently conflicting observations, common in the literature, regarding territoriality. The increase in aggression in early trials of video playbacks is reminiscent of previous lizard and bird studies reporting that a single agonistic interaction with another male conspecific increases territorial aggression during and immediately after the interaction (Moore 1987; Thompson & Moore 1992; Wingfield 1994). Conversely, the decline in aggression in later video playback trials is consistent with the 'dear enemy' phenomenon reported in diverse taxa (in fish, Johnsson 1997; in frogs, Burmeister et al. 1999; in *Anolis* lizards, Qualls & Jaeger 1991; in lizards, Fox & Baird 1992; Whiting 1999; for a review, see Temeles 1994). We note that the reduced aggressive responses in later video playback trials do not indicate the exact aspect of the stimulus that releases this pattern – for example, individual recognition of the male in the video vs. the repetitive nature of video presentation. The former is more consistent with the 'dear enemy' phenomenon, while the latter relates to general response habituation.

Habituation, the general term for a decline in the response to a specific stimulus, may explain the reduced aggressive responses towards the video stimuli during the later playback trials. Habituation is characterized by stimulus and response specificity (Thompson & Spencer 1966; Domjan 1998). The 'dear enemy' phenomenon is often thought of as more complex than simple stimulus habituation, because it involves decisions based on individual recognition of familiar neighbors. However, use of the habituation/dishabituation paradigm for the recognition of natural stimuli demonstrates habituation to many complex attributes (reviewed in Hauser 1996; chapter 7). The emergence of social memory in rodents, for example, can be observed by presenting individual animals to subjects on successive days; repeated presentations quickly lead to a decline in investigation of the individuals, which is restored by the presentation of a novel individual. Similarly, vervet monkeys habituate to repeated presentations of 'wrr' calls from a single individual – calls that are associated with aggression. This behavioral habituation generalizes to 'chutter' calls from the same individual, which convey a similar meaning, but not to the 'wrr' calls of other individuals (Cheney & Seyfarth 1988). The habituation/dishabituation paradigm has also been used to investigate the recognition of natural signals in many other taxa, including ground squirrels (Hare 1998), giant pandas (Swaigood et al. 1999) and golden hamsters (Mateo & Johnston 2000). These studies demonstrate that habituation and individual recognition are by no means mutually exclusive. Indeed, habituation to the presence and aggressive signaling of neighbors may prove to be a mechanism translating individual recognition into the tolerance of a 'dear enemy.'

Data from this experiment alone are insufficient to conclude that individual recognition and/or the 'dear enemy' phenomenon led to a decrease in aggressive response to the video stimulus at later trials. Further examination by using a different stimulus male each time in the video clip should ameliorate the ambiguity as to which specific aspect of stimulus the animals habituate their responses. However, it seems unlikely that animals only habituate to the

repetitive presentation of the same video clip, while remaining responsive to the stimulus male on the video. Repetitive exposure to a live conspecific male also leads to a decrease in aggressive response following a transient increase from subject animals (Yang & Wilczynski, unpubl. data). In addition, this behavioral pattern follows a similar time course to that reported here-in. Habituation to live conspecific anoles was also found by Qualls & Jaeger (1991).

Anoles in both groups displayed little aggression during the last video playback, but both groups were aggressive towards the live stimulus animal. However, animals with five daily aggressive encounters showed more aggressive responses towards novel live conspecifics than did controls. This result is in accordance with several studies demonstrating that the prior experience of an individual significantly influences its territorial aggression towards conspecific intruders. For example, when subjected to interrupted or incomplete aggressive encounters for several days, mice showed increases in aggression (Leshner & Nock 1976). Stamps & Krishnan (1994a, 1998) showed that the number of opponents that an anole had during territory settlement is the most important factor for predicting its future behavior in an aggressive encounter. In addition, in a study of green anoles, Greenberg et al. (1984) found that the outcome of a single aggressive encounter, whether being dominant or subordinate, influences later aggressive behaviors of animals. Furthermore, fighting experience during an individual's development is highly associated with that individual's final status and space use (Stamps & Krishnan 1998).

Although our findings are consistent with experience-mediated changes observed in many taxa, the proximate basis for experience-potentiated aggression remains unclear. One possibility is that aggression is reinforcing. Thompson (1963) demonstrated that Siamese fighting fish (*Betta splendens*) will work for the opportunity to display aggression. Analogous studies have been carried out with other fishes (Rasa 1971; Gerlai & Hogan 1992; Losey & Sevenster 1995) and with mice (Ginsburg & Allee 1942; Legrand 1970, 1978; Martinez et al. 1995). Interestingly, many of the studies investigating the reinforcement properties of successful aggression also report habituation to the test stimulus (Baenninger 1970; Melvin & Anson 1970; Gerlai & Hogan 1992), suggesting that our findings may generalize to other taxa.

Despite the general finding that the opportunity to perform aggression can be positively reinforcing, the source of this reinforcement remains controversial. A number of authors argue that these studies attribute rewarding features to aggressive experience that may be more appropriately attributed to social contact in general (Legrand 1978; Taylor 1979; Bronstein 1981). However, the reward properties of general social interaction do not seem to explain the repeated finding that animals who are dominant, aggressively experienced, or primed with a preliminary fight, are more likely to find aggressive interactions reinforcing (Baenninger 1970; Legrand 1970, 1978; Taylor 1979). A more viable alternative is that the conspecific stimuli serve as releasers, and that it is the disappearance or cessation of the releaser that reinforces aggression. For

example, in three-spined sticklebacks, associating a male's head-down threat display with the disappearance of an opponent leads to an increased use of this particular aggressive signal (Losey & Sevenster 1995). This is consistent with the assertion that performing aggressive displays may actually be aversive (Stamps & Krishnan 1999). Thus behaviors leading to victory are reinforced by virtue of eliminating aversive interactions. Because the claim that aggression is reinforcing is generally limited to victorious experience, defined by the cessation of opposition, the two most viable explanations seem to be functionally equivalent. Determining whether either process produces the experience-dependent changes observed in our subjects will require further study.

Our data indicate that 'stressfulness' co-varied with aggression during the video playback trials, but could not explain group differences during exposure to a novel male. Specifically, the animals shown the aggression video exhibited darker colorations during the third video playback, when aggression was much higher in the aggression video group than in the control group (Fig. 3). This result is consistent with studies in birds, which demonstrated that after being exposed to the simulated intrusion of a conspecific male for 10 min, male territorial birds showed increases in plasma corticosterone level, a physiological indicator of stress (Silverin 1993; Astheimer et al. 2000). During our test with a live conspecific, lizards from both groups displayed aggressive behavior, and both groups showed morphological indicators of a stress response. This stress response was not significantly different in the two groups, even though the animals exposed to the aggressive video showed much more aggression.

Contrary to our findings, a number of studies suggest a negative association between aggression and stress (Wingfield & Silverin 1986; Tokarz 1987; Denardo & Licht 1993; but see Astheimer et al. 2000). The discrepancies between our results and those of previous studies can be attributed to differences in the length and type of stress. Most social stress studies are concerned with long-term defeat experience or subordinate status leading to chronic stress (Greenberg et al. 1984; for review, Sapolsky 1991; Summers & Greenberg 1994; Blanchard et al. 1998). In our study, interactions with the aggressive stimulus video generated stress, but these exposures were brief and could not result in unambiguous defeat. However, we could not exclude the possibility that changes in morphological indicators of stress in our results may not be perfectly correlated with physiological stress responses, which are more appropriate for testing long-term vs. short-term stress responses. This possibility should be clarified by investigations measuring endocrine responses, such as levels of circulating catecholamines or corticosterone over this type of experience and subsequent tests with a novel conspecific.

Our data highlight the importance of distinguishing between the processes invoked during territory acquisition and territory maintenance. It has been reported, for example, that animals exhibit increased aggression during the early stages of territorial acquisition to establish territories or social relationships with other conspecifics (Mackintosh 1970; Stamps & Krishnan 1998).

After resolving the dispute with a conspecific, aggressive interaction between members of a dyad dramatically decreases (Crews 1978; Stamps & Krishnan 1994b, 1999). However, when a strange conspecific enters one's territory, aggressive behavior recurs. Taken together, our results suggest that the conflicting demands on aggression may be resolved by two common perceptual processes. The first is an experience-dependent increase in aggression that accompanies territory acquisition, perhaps mediated by reinforcement mechanisms. The second is habituation to frequently encountered signals, which reduces aggression towards familiar animals in familiar contexts, and yet does not prevent a territory owner from being aggressive to a novel challenger. Evolutionary adjustments of the parameters involved in these perceptual processes may suffice to explain a great deal of the context specificity evident in natural territorial behavior.

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