

Ryan L. Earley · Megan Tinsley · Lee Alan Dugatkin

## To see or not to see: does previewing a future opponent affect the contest behavior of green swordtail males (*Xiphophorus helleri*)?

Received: 12 December 2002 / Accepted: 13 March 2003 / Published online: 23 April 2003  
© Springer-Verlag 2003

**Abstract** Animals assess the fighting ability of conspecifics either by engaging in aggressive interactions or observing contests between others. However, whether individuals assess physical prowess outside the context of aggressive interactions remains unknown. We examined whether male green swordtails (*Xiphophorus helleri*) extract information about the fighting ability of solitary individuals via observation and whether acquiring such information elicits behavioral modifications. Contests preceded by mutual visual assessment were significantly shorter than fights where only one or neither of the two individuals was informed in advance. Focal animals initiated aggressive behavior more often against larger opponents only after previewing their adversary, indicating that swordtails can extract information about relative body size from watching solitary conspecifics. When a fighting disadvantage is perceived, observers adopt tactics that increase their probability of winning the contest.

### Introduction

Existing models of animal combat examine how assessment of relative fighting ability mediates individual decisions to continue to fight or retreat (Enquist and

Leimar 1983; Enquist et al. 1990; Payne and Pagel 1997; Mesterton-Gibbons and Adams 1998; Payne 1998). A common assumption among these models, and accompanying empirical tests, is that individuals gain all information about an opponent's physical prowess during the contest itself. However, recent developments in communication networks demonstrate that animals acquire information about the fighting ability of conspecifics by watching aggressive contests, a phenomenon known as eavesdropping (McGregor and Peake 2000). In fishes, visual cues provide a gauge of relative status and allow eavesdroppers to make an independent assessment of the watched contestants' fighting ability (Oliveira et al. 1998; McGregor et al. 2001; Earley and Dugatkin 2002). An interesting question that remains unexplained is whether information independent of opponent fighting tactics is useful to an observer. Will observers cue on characteristics of a solitary conspecific and use this information in subsequent encounters with that individual?

Animals in social groups may have equal or greater opportunity to watch individuals as they do dyads and, as a consequence, may benefit from gathering subtle cues indicative of fighting ability (e.g., body size). For instance, female domestic fowl prefer dominant males irrespective of morphology when given opportunity to assess male fighting ability by observing rank-order interactions (Graves et al. 1985). In the absence of opportunities to observe male social interactions, females prefer males possessing traits associated with high rank (e.g., comb area, Graves et al. 1985).

In this study, we investigate whether early, asymmetrical information acquisition, outside the context of observing an aggressive interaction between others, influences contest dynamics in male *X. helleri*. Although several morphological and behavioral cues may be available to an observer, we concentrated primarily on small differences in size (e.g., body length, body depth, and sword length). By comparing this study on *X. helleri* to those that have investigated eavesdropping on aggressive contests, we have the opportunity to distinguish the effects of integrating individual versus contest-related

---

R. L. Earley (✉) · L. A. Dugatkin  
Department of Biology, Life Sciences Building,  
University of Louisville, Louisville, KY 40292, USA  
e-mail: biorle@langate.gsu.edu  
Tel.: +1-404-6514347  
Fax: +1-404-6513929

M. Tinsley  
Department of Ecology and Evolutionary Biology,  
University of Tennessee,  
Knoxville, TN 37996, USA

#### Present address:

R. L. Earley, Department of Biology,  
Georgia State University,  
402 Kell Hall, MSC 8L0389, 33 Gilmer St. SE,  
Unit 8, Atlanta, GA 30303-3088, USA

cues. Consequently, we can predict how information acquisition translates into modifications of an observer's behavioral repertoire.

## Methods

*Xiphophorus helleri* were obtained in heterosexual groups from Sunshine Aquatic Farms (Tampa, Fla.) and kept in large aquariums (189–429 l). Holding tanks were equipped with chemical and biological filtration, aeration, gravel substrate at depth 6 cm, and refugia. Temperature was maintained between 25–27°C, pH 7.6, and photoperiod at 12 h light:12 h dark. Fish were fed TetraMin flake food daily with occasional supplements of brine shrimp.

Males were removed from the holding tanks, and body length, sword length, and body depth were measured to calculate lateral surface area [(body length × body depth) + sword length]. Two fish were matched for lateral surface area (<0.2 units difference), placed in individual isolation tanks (8 l) for 48 h, and then transferred to experimental tanks (38 l) that were divided into two compartments of equal size. Both compartments were equipped with aeration and heating devices positioned behind porous partitions to prevent the fish from taking refuge during the trials. The two fish were visually isolated from one another by an opaque divider that masked one of three additional partitions: a second opaque plastic divider (Opaque treatment), one-way mirror (Mirror treatment), or clear glass (Clear treatment). A 60-W incandescent bulb located approximately 16 cm above the experimental aquariums provided illumination. Behavioral observations began after 16 h of acclimatization to the experimental aquarium. The acclimatization and isolation periods (i.e., 64 h of visual isolation) aimed to minimize the effects of previous fighting experience in the communal tanks; behavioral effects of past wins or losses persist for at least 24 h in *X. helleri* (Franck and Ribowski 1987).

A 1-h observation trial began when the divider masking the opaque, one-way mirror, or clear partitions was removed. Each contestant remained visually isolated from its opponent in the Opaque treatment. In the Clear treatment, the contestants could interact and visually assess one another across the glass partition. We recorded the number of aggressive and submissive acts exhibited across the glass divider and, if applicable, the time of contest settlement and the winner/loser of the cross-partition interaction (see Franck and Ribowski 1989 for behavioral descriptions). In the Mirror treatment, the light was placed at a 45° angle above the naïve contestant's compartment so that the observer could view its opponent without being detected. Tint was placed over the mirror side of the one-way glass to minimize reflection and eliminate the possibility that the naïve contestant could respond to its mirror image. This lighting regime did not have any detectable effects on the activity levels of the experimental fish. To negate side-biases, the observer was placed on the left and right sides of the aquarium in an equivalent number of trials. We minimized transfer of chemical/olfactory cues between fish in all treatments by fitting the partitions tightly against the aquarium walls without compromising easy removal.

After the observation period, the partition separating the focal fish from its opponent was removed to facilitate a dyadic 'focal' contest. Lifting the partition between the contestants minimizes the potential effects of handling (e.g., transfer to a new aquarium by netting), which may elicit physiological changes that influence agonistic behavior (Rotllant and Tort 1997; Overli et al. 1999). The fish were allowed to interact for 1 h, during which time the latency to and frequency of all aggressive (approach, threat display, attack, bite) and submissive (avoid, retreat) behavior as well as the identity of the aggressor and recipient, the number of mouth-wrestling bouts and reciprocal acts, contest duration, and the subsequent winner and loser were recorded. The fish that directed aggression toward its opponent at least ten times without reciprocation was designated the dominant animal (Francis 1983). Both the observation trial and the focal contests were videotaped for analysis. Thirty trials per treatment were conducted and new fish were used in each trial (90

total trials; 180 fish). For the purposes of statistical inquiry, the observer in the Mirror treatment was designated as the focal individual. Since both contestants in the Clear and Opaque conditions received the same treatment, we tossed a coin to determine the focal individual.

## Treatment comparisons

In both the Mirror and Opaque treatments, at least one individual was naïve to the presence of its future opponent. Only in the Mirror treatment could the second individual observe and become familiar with cues relevant to its opponent's fighting ability. Differences in focal contest dynamics between the Mirror and Opaque treatments indicate that previewing an opponent influences an observer's subsequent behavior. Similarly, in both the Mirror and Clear treatments, at least one individual could visually assess its opponent across the partition. Only in the Clear treatment could both subjects interact. Comparisons between the Mirror and Clear treatments elucidate the effects of cross-partition interaction. Interactions could alter focal contest dynamics via several mechanisms; individual recognition or reinstatement of the dominance relationship established across the glass partition, both of which are part and parcel of the interaction itself, are likely candidates (e.g., Beaugrand 1997).

## Results

### Effects of size

The effect of lateral surface area on contest outcome was homogeneous across treatments (heterogeneity;  $G_2=0.6$ ,  $P=0.75$ ). The pooled data revealed that small differences in lateral surface area (<0.2 units) have negligible effects on contest outcome ( $G_1=0.2$ ,  $P=0.67$ ); larger individuals won 42 of the 88 contests in which the opponents differed in size (two contests occurred between individuals with the same lateral surface area).

### Initiation behavior and contest outcome

Log-linear analyses tested differences among treatments in the focal individual's propensity to initiate approach, threat display, attack, or bite and to win the focal contest. The probability of focal individual initiation was homogeneous across treatments for all types of aggressive behavior (Table 1). Focal individuals also won the same proportion of contests across treatments (Table 1). Pooled treatment data indicated that focal and non-focal subjects were equally likely to initiate all types of aggression and to win disputes (Table 1). There were no significant treatment differences in mean latencies to first approach, threat display, attack, or bite (multivariate ANOVA;  $F_{8, 150}=1.1$ ,  $P=0.34$ ). Initiators of threat display, attack, and bite won most focal contests but significantly more so when the contests did not escalate (escalated versus non-escalated;  $G_1>10.5$ ,  $P<0.0012$ ; Table 1); approach initiation showed no such pattern. In the Clear treatment, focal contest outcome was influenced by interactions across the glass partition. Of the 22 pairs that established a dominance relationship across the partition, 18 maintained this relationship in the focal fight ( $G_1=5.1$ ,  $P=0.02$ ).

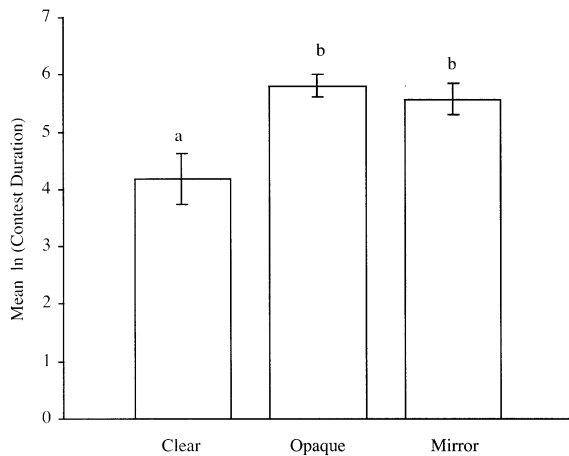
**Table 1** Treatment differences in focal contest characteristics. *G*-tests were used for all comparisons with heterogeneity  $df=2$ , pooled  $df=1$ . When the three treatments were homogeneous ( $G_2 < 3.3$ ,  $P > 0.05$ ), only the pooled data are shown

Parameter	Treatment	Yes	No	NA <sup>a</sup>	<i>P</i>
Focal fish initiates approach	Pooled	45	45		ns <sup>b</sup>
Focal fish initiates threat display	Pooled	42	47	1	ns
Focal fish initiates attack	Pooled	44	40	6	ns
Focal fish initiates bite	Pooled	47	39	4	ns
Focal fish wins	Pooled	49	41		ns
Focal contest escalates	Mirror	15	15		
	Clear	11	19		
	Opaque	23	7		
	Heterogeneity				<0.01
	Pooled	— <sup>c</sup>	— <sup>c</sup>		— <sup>c</sup>
Initiator of threat display wins, non-escalated	Pooled	35	5	1	<0.0001
Initiator of threat display wins, escalated	Pooled	28	21		ns
Initiator of attack wins, non-escalated	Pooled	36	0	5	<0.0001
Initiator of attack wins, escalated	Pooled	32	16	1	<0.05
Initiator of bite wins, non-escalated	Pooled	36	2	3	<0.0001
Initiator of bite wins, escalated	Pooled	26	22	1	ns

<sup>a</sup> NA: neither contestant initiated the focal behavior during the fight

<sup>b</sup> ns:  $p > 0.05$

<sup>c</sup> Pooling data is not warranted given significant treatment heterogeneity – see text for analysis

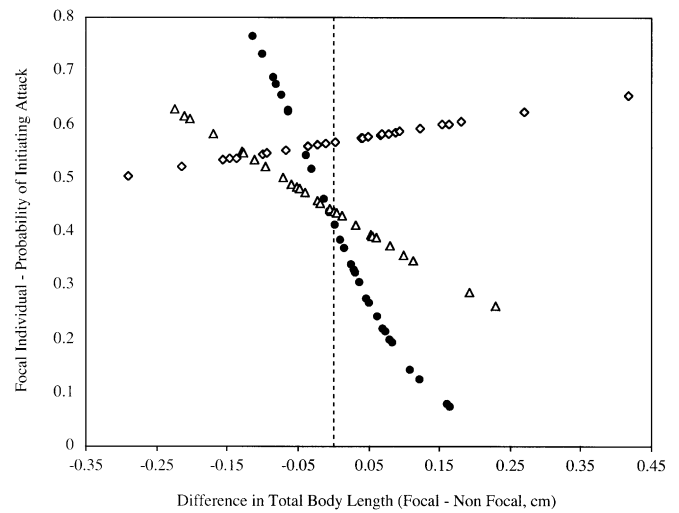


**Fig. 1** Treatment differences in contest duration (s); bars labeled with different letters are statistically different from one another at the  $P < 0.05$  level (SNK). Error bars represent mean  $\pm$  SEM (SEM: Clear = 0.438, Opaque=0.195, Mirror=0.283)

### Contest duration and escalation

Escalated contests involved mouth-wrestling, circle biting, or prolonged bouts of mutual threat display (>15 bouts). The probability of contest escalation was heterogeneous across treatments (Table 1). Treatment differences were assessed using a two-tailed Tukey's test of proportions (critical value:  $q_{0.05, \alpha, 3(2)} = 3.31$ ; Zar 1996). Escalated contests occurred significantly more often in the Opaque than the Clear treatment ( $q = 4.4$ ,  $P < 0.05$ ). The proportion of escalated contests in the Mirror treatment did not differ significantly from the Clear ( $q = 1.4$ ,  $P > 0.05$ ) or Opaque ( $q = 3.0$ ,  $P > 0.05$ ) treatments.

A multivariate ANOVA tested treatment differences in several parameters related to contest intensity (e.g., duration, total aggressive acts, total agonistic bouts, ratio of high- to low-intensity interactions). Assumptions of normality were met and there were significant treatment



**Fig. 2** The relationship between the focal individual's probability of initiating attack in the focal contest and differences in total body length (cm) between the focal and non-focal fish in the Mirror (solid circles), Clear (empty triangles), and Opaque (empty diamonds) treatments using a logistic regression analysis. Negative/positive values on the abscissa indicate that the focal fish was smaller/larger than its future opponent; the dashed line crosses the abscissa at zero

differences (Pillai's trace:  $F_{22, 156} = 2.1$ ,  $P = 0.006$ ). The only significant parameter after Dunn-Sidak adjustments was contest duration, which was natural log-transformed ( $F_{2, 87} = 7.5$ ,  $P = 0.001$ ). Contest duration was defined as the time elapsed between contest initiation and settlement. The duration of contests in the Opaque and Mirror treatments was similar and significantly longer than contests in the Clear treatment (Student-Newman-Keuls test, SNK;  $P < 0.05$ ) (Fig. 1).

## Potential cues

Small differences in sword length, body depth, and body length existed despite the contestants being matched for lateral surface area. Focal fish initiated attack significantly more often against individuals whose body length exceeded their own, but only after having previewed their opponent (length  $\times$  treatment; Mirror vs. Opaque:  $\chi_1^2=3.9$ ,  $P=0.048$ ) (Fig. 2). No significant relationships emerged between initiation of approach, threat display, or bite and any of the body size parameters ( $\chi_1^2<3.5$ ,  $P>0.06$ ).

---

## Discussion

In this study we determined whether male *X. helleri* extract information about fighting ability by observing solitary conspecifics and whether acquiring this information generates changes in behavior. When differences in body size between the opponents were not considered, observation alone did not appear to influence contest dynamics. However, when characters related to body size were examined as putative indicators of fighting ability, treatment differences emerged. Swordtail observers were able to detect small disparities in relative body size. Observers initiated aggression significantly more often when their opponent's body length exceeded their own and the propensity to initiate increased with the magnitude of the size difference. Changes in motivation to attack as a function of relative body size appear to be triggered by observing solitary conspecifics, particularly because such changes occurred in the Mirror treatment but not the Opaque treatment. Initiators of attack won the focal contests significantly more often than non-initiators, suggesting that rapid escalation is effective at deterring opponents. Thus, when a fighting disadvantage is perceived, smaller observers adopt tactics that are likely to increase contest success.

Our data correspond well with earlier studies on contest behavior in *X. helleri*. Subordinate males from stable dominance hierarchies exhibit higher frequencies of aggression toward mirror-image stimuli, escalate faster, and display higher rates of aggressive behavior during the initial stages of a contest than dominant animals do (Franck and Ribowski 1987, 1989; Ribowski and Franck 1993). But why should subordinates or individuals who perceive themselves to be smaller have a greater penchant for escalatory behavior? In the hierarchical social system of swordtails, dominant males exclude small subordinates from mating opportunities and often inhibit sexual maturation (Beaugrand et al. 1984; Borowsky 1987). Because low status likely bears a high cost, smaller animals may initiate aggression in an attempt to deter their opponent and potentially increase their status. Large dominant animals may opt against initiating aggressive interactions in the interest of preserving status, particularly when the opponent is only slightly smaller. Initiating attack confers the greatest

advantage in non-escalated interactions but is an effective predictor of contest success even under escalated circumstances. The overall high prospects of winning and the potential benefits accrued increased status and mating opportunity may outweigh the risks of initiating attack (e.g. time, energy, injury, or defeat if the opponent retaliates) for smaller animals. The opposite may apply to initiating threat displays and bites, both of which increase contest success only in non-escalated bouts. Differences in the likelihood of winning relative to the costs of escalation may explain why observers show a sharp change in attack behavior but not threat display or biting after previewing slightly larger opponents.

In future studies of this nature, it may be useful to increase size asymmetries between focal and non-focal animals and to examine additional characters and/or signals indicative of physical prowess. Amplifying the size variation between the opponents may increase the capacity of the observer to visually detect differences in relative fighting ability and may better mimic natural social conditions. Exploring an observer's response to characters such as pigmentation patterns (e.g., vertical bars, Morris et al. 1995) or experience-specific postures or coloration (e.g., subordinates flatten the dorsal fin against the body and adopt darker coloration patterns) may aid in gaining a comprehensive understanding of how observers integrate and utilize visual cues from their social environment. Manipulating asymmetries in size, pigmentation patterns, or previous social experience may reveal that observers adjust their behavioral repertoire in a context-dependent fashion to a host of characters indicative of strength, motivational state, or past contest success.

Prior interaction between the focal and non-focal fish had a substantial impact on contest dynamics. Contests in the Clear treatment were significantly shorter and escalated less than those in the Opaque or Mirror treatments. Dominance relationships established across the glass partition were maintained in a majority of the focal contests. These data provide evidence that visual cues, the predominant means of assessment across the glass partition, carry accurate information about relative fighting ability and are used effectively to settle disputes. Similar results exist for cichlid fish (Enquist et al. 1987; Keeley and Grant 1993) and rainbow trout (Johnsson and Åkerman 1998). Because the fish engaged in mutual assessment during the observation phase, the need for prolonged focal contests was reduced, if not abolished. Our results provide further support for the prediction that contests between familiar adversaries should be shorter and less escalated than interactions between unfamiliar opponents (Enquist et al. 1987; Keeley and Grant 1993; Beaugrand 1997; Johnsson and Åkerman 1998).

In conclusion, our data demonstrate that swordtails extract relevant information about the fighting ability of solitary conspecifics, and change their behavior in ways that potentially maximize contest success. The communication network concept focuses on the ability of animals to gather information from signaling *interactions* between

others (McGregor and Peake 2000). Gaining information from solitary conspecifics may also be an important component of the network. Though direct interactions likely provide the most accurate information about relative fighting ability, indirect information obtained by observing fights or solitary individuals also modulates the agonistic decisions of swordtail males (Earley and Dugatkin 2002). Integrating direct experience with observational information may reduce the probability of erroneous agonistic decisions and allow individuals to adopt strategies that enhance fighting success (e.g., Peake et al. 2002).

**Acknowledgements** We thank Blair Gilliland for assistance in data transcription, Michael Boles, Matthew Druen, Trish Sevene-Adams, Matthew Grober, Gordon Schuett, Justin LaManna, and several anonymous referees for enlightening suggestions, and the Animal Behavior Society, Kentucky Academy of Science, and National Science Foundation for funding. This research followed the Guidelines for the Use of Animals in Research (IACUC no. 98050 at the University of Louisville).

## References

- Beaugrand JP (1997) Resolution of agonistic conflicts in dyads of acquainted green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae): a game with perfect information. *Behav Proc* 41:79–96
- Beaugrand JP, Caron J, Comeau L (1984) Social organization of small heterosexual groups of green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae) under conditions of captivity. *Behaviour* 91:24–60
- Borowsky RL (1987) Agonistic behavior and social inhibition of maturation in fishes of the genus *Xiphophorus* (Poeciliidae). *Copeia* 1987:792–796
- Earley RL, Dugatkin LA (2002) Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. *Proc R Soc Lond B* 269:943–952
- Enquist M, Leimar O (1983) Evolution of fighting behaviour: decision rules and assessment of relative strength. *J Theor Biol* 102:387–410
- Enquist M, Ljungberg T, Zandor A (1987) Visual assessment of fighting ability in the cichlid fish *Nannacara anomala*. *Anim Behav* 35:1262–1263
- Enquist M, Leimar O, Ljungberg T, Mallner Y, Segerdahl N (1990) A test of the sequential assessment game: fighting in the cichlid fish, *Nannacara anomala*. *Anim Behav* 40:1–14
- Francis RC (1983) Experiential effects on agonistic behavior in the paradise fish, *Macropodus opercularis*. *Behaviour* 85:292–313
- Franck D, Ribowski A (1987) Influences of prior agonistic experiences on aggression measures in the male swordtail (*Xiphophorus helleri*). *Behaviour* 103: 217–240
- Franck D, Ribowski A (1989) Escalating fights for rank-order position between male swordtails (*Xiphophorus helleri*): effects of prior rank-order experience and information transfer. *Behav Ecol Sociobiol* 24:133–143
- Graves HB, Hable CP, Jenkins TH (1985) Sexual selection in *Gallus*: effects of morphology and dominance on female spatial behavior. *Behav Proc* 11:189–197
- Johnsson J, Åkerman A (1998) Watch and learn: preview of the fighting ability of opponents alters contest behaviour in rainbow trout. *Anim Behav* 56:771–776
- Keeley ER, Grant JWA (1993) Visual information, resource value, and sequential assessment in convict cichlid (*Cichlasoma nigrofasciatum*) contests. *Behav Ecol* 4:345–349
- McGregor PK, Peake TM (2000) Communication networks: social environments for receiving and signalling behavior. *Acta Ethol* 2:71–81
- McGregor PK, Peake TM, Lampe HM (2001) Fighting fish *Betta splendens* extract relative information from apparent interactions: what happens when what you see isn't what you get. *Anim Behav* 62:1059–1065
- Mesterton-Gibbons M, Adams E (1998) Animal contests as evolutionary games. *Am Sci* 86:334–341
- Morris MR, Mussel M, Ryan MJ (1995) Vertical bars on male *Xiphophorus multilineatus*: a signal that deters rival males and attracts females. *Behav Ecol* 6:274–279
- Oliveira RF, McGregor PK, Latruffe C (1998) Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc R Soc Lond B* 265:1045–1049
- Overli O, Olsen RE, Lovik F, Ringo E (1999) Dominance hierarchies in Arctic charr, *Salvelinus alpinus* L.: differential cortisol profiles of dominant and subordinate individuals after handling stress. *Aquac Res* 30:259–264
- Payne R (1998) Gradually escalating fights and displays: the cumulative assessment model. *Anim Behav* 56:651–662
- Payne R, Pagel M (1997) Why do animals repeat displays? *Anim Behav* 54:109–119
- Peake TM, Terry AMR, McGregor PK, Dabelsteen T (2002) Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proc R Soc Lond B* 269:1925–1929
- Ribowski A, Franck D (1993) Subordinate swordtail males escalate faster than dominants: a failure of the social conditioning principle. *Aggress Behav* 19:223–229
- Rotllant J, Tort L (1997) Cortisol and glucose responses after acute stress by net handling in the spard red porgy previously subjected to crowding stress. *J Fish Biol* 51:21–28
- Zar JH (1996) *Biostatistical analysis*, 3rd edn. Prentice Hall, Englewood Cliffs, N.J.