PREY FLIGHT BEHAVIORS IN RESPONSE TO WADING BIRD DISTURBANCES

AND THEIR INFLUENCE ON FORAGING STRATEGY OF

GREAT BLUE HERONS (<u>Ardea</u> <u>herodias</u>)

by

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A THESIS

APPROVED:_____
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An Abstract of the Thesis of

Douglas Robert Warrick for the degree of Master of Science

in the Department of Biology   to be taken   August 1992

Title: PREY FLIGHT BEHAVIORS IN RESPONSE TO WADING BIRD

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A geometric model using idealized prey behaviors in reaction to wading bird disturbances was developed to hypothesize how wading bird foraging strategy might most efficiently counter those behaviors. The model suggests that for prey responding to wading bird disturbances with flight response distance strongly negatively correlated to their distance from the point of disturbance, wading birds could employ disturbance facilitated social foraging strategy, thereby increasing individual foraging efficiency and selecting for social foraging.

In controlled studies of the reactive behaviors of two primary prey species seen to be taken at disparate rates by solitary and socially foraging herons, schooling Shiner Surfperch exhibited behaviors favoring social foraging in herons, while Staghorn Sculpins exhibited no correlation in

their flight response distances relative to their proximity to the disturbance, and seemed unlikely to be more efficiently utilized by socially foraging wading birds.

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ACKNOWLEDGMENTS

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CHAPTER I

INTRODUCTION

Within the paradigmic framework of optimal foraging theory exist the descriptions of mechanisms selecting for territorial or social foraging strategies. The refinement of the models describing these mechanisms and the empirical evidence to support those models have focused primarily on the foraging ecology of granivorous, insectivorous, and nectivorous birds (eg. Horn 1968; Crook 1965; Cody 1971; Thompson et. al. 1974; Gill and Wolf 1975; Carpenter and MacMillen 1976). Summarized, these studies indicate that social foraging should be selected for when the resource is patchy and unpredictable, and that territoriality should occur when the resource is predictable, appropriable, and evenly distributed.

Few studies of predators foraging for behaviorally sophisticated prey have been conducted to test how well these predatory species conform to the predictions offered by the aforementioned foraging models. Prey behavior is discussed tangentially when wading bird ecologists describe the potential increase in foraging efficiency of individuals within a group via disturbance facilitated foraging. Here,

individuals in a group benefit from the otherwise unavailable that prey are driven from refuges by the foraging activity of the other individuals. While this has been demonstrated by Kushlan (1978b) in the case of the Little Blue Heron (<u>Florida</u> <u>caerulea</u>) taking invertebrate prey disturbed by the foraging activities of the White Ibis (<u>Eudodocimus</u> <u>albus</u>), few instances of this phenomenon have been describe for wading birds foraging for more active and sophisticated prey. Krebs (1974), in a study of Great Blue Herons (<u>Ardea</u> <u>herodias</u>), noted that though the rate of fish capture increased with flock size, foraging efficiency did not increase with flock size for a given number of fish. He therefore concluded that social foraging was merely a strategy for finding and exploiting ephemeral, highly clumped and patchy fish resources, which was consistent with existing foraging models. (It should be noted, however, that in this discussion, which was in fact a discussion of fish behavior as well as heron foraging, no mention was made of fish species.) Krebs also noted that the individuals in such a foraging flock maintained large individual distances, suggesting that wading birds dependant upon stealth, may, by disturbing prey, hinder each other's efforts by foraging too closely together. This apparent compromise between social foraging as a means to find concentrations of prey and the need to minimize the disturbance created by large aggregations was taken a step further by Kushlan (1978a) who

proposed that for some wading birds foraging efficiency should increase with flock size (independent of prey abundance, contrary to Krebs observations) to a maximum determined by the increase in interference. Again, little attention has been given to the prey type and its behavior in these studies; without this, it seems dangerous to suggest that social foragers could maintain individual distances to prevent interference while at the same time derive some disturbance facilitated foraging benefit (eg. via driving or herding prey) from their relatively close proximity. Sih (1984), in examining the relationship of the Hemipteran Notonecta and its mosquito larvae prey, has demonstrated that prey evasive behaviors can have a profound effect on predator foraging. However, any further speculation on these types of effects in regard to wading birds and their prey are pointless without an understanding of the behaviors of those prey. It was the purpose of this study to investigate those prey behaviors and determine their possible influence on the foraging strategy of a wading bird.

A population of Great Blue Herons in the Coos Bay estuary, Oregon, was selected for a study composed of three parts:

Chapter II. Hypothesize what behaviors prey would need to exhibit to respectively select for social and solitary foraging.

Chapter III. Determine the important fish prey species for Great Blue Herons in the Coos Estuary.

Chapter IV. Determine if a disparity exists in foraging efficiency between solitary and socially foraging herons when foraging for each of those species.

Chapter V. Using those prey species shown to be taken at disparate efficiencies by solitary and social herons, a study of prey flight behaviors would be conducted. The controlled experiments were designed to illustrate those fishes conformity to the predictions made by the prey reactive behavior models (Chapter II) and foraging observed in Coos Bay Estuary herons (Chapter IV). The behaviors selected for study were: (1) Threshold of reaction to a heron disturbance; (2) evasive flight distance and (3) schooling behavior.

CHAPTER II

PREY FLIGHT BEHAVIOR MODEL

The geometric model in Figure 1 represents idealized prey evasive behaviors in reaction to a wading bird disturbance. It assumes the following:

(1) The greatest disturbance created by a heron foraging for mobile, behaviorally sophisticated prey is the strike, or capture attempt. The basis for this assumption is in the foraging tactics of Great Blue Herons. Once arriving at a foraging site, the most commonly employed feeding tactic is the "Slow walk" and "Stand and Wait," (Hancock and Kushlan 1984; pers. obs; after Meyerriecks 1960,); the underpinning of both tactics is stealth. Furthermore, after a strike, successful or not, herons often walk quickly away, generally more than 2-3 m, before resuming a stealthy search.

(2) Prey reaction (flight response) will be negatively correlated to the prey's distance from the disturbance, i.e., those prey closer to the disturbance will react more strongly than those farther away.

(3) Prey flight response will be directly away from
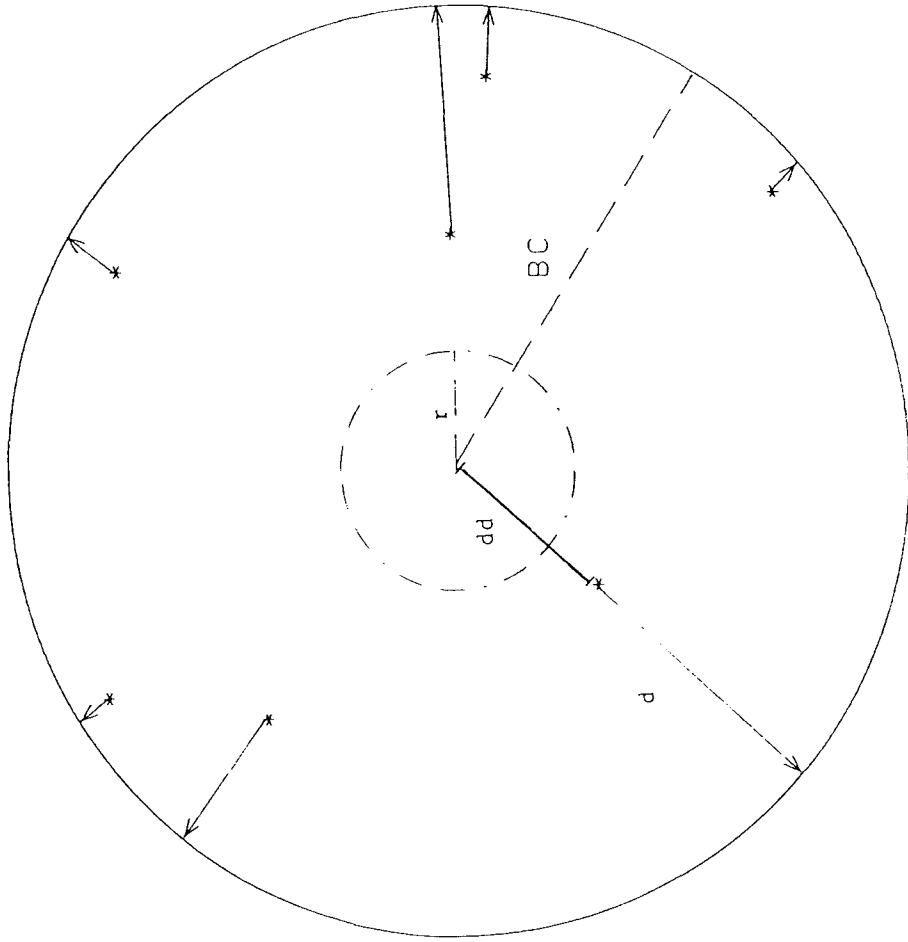
Figure 1. Hypothetical prey bomb crater effect.

the point of disturbance would result in the prey
stopping their evasive burst on the perimeter of the
circle *bc*.

(4) An absence of prey refuge.

With a negative linear relationship of distance from
the disturbance (*dd*) and flight distance (*d*), the sum of
these conditions would result in a localized "bomb crater"
(*bc*) effect as illustrated in Figure 1, with the heron
strike radius *r*, with non-schooling prey distributed on the
circumference of the circle *bc*, and schooling prey
presumably re-schooling somewhere along the perimeter.

In response to such prey behavior, wading birds could
maximize their foraging efficiency in several ways. As
illustrated in Figure 2, non-schooling prey could be
"driven" by a solitary heron employing the "square search."
After the first strike disturbance, the heron simply walks
to position 2, where it encounters the concentration of prey
near the perimeter of the circle *bc*. Striking and again
disturbing prey into another circle, it turns perpendicular
its last direction of movement. As this tactic is repeated,
prey would become concentrated as shown, thereby increasing
foraging efficiency.

Non-schooling prey responding in the circle *bc* fashion
would also be susceptible to disturbance facilitated
foraging by two or more herons. By situating themselves
such that each of their strike radii (circles *r*) would lie
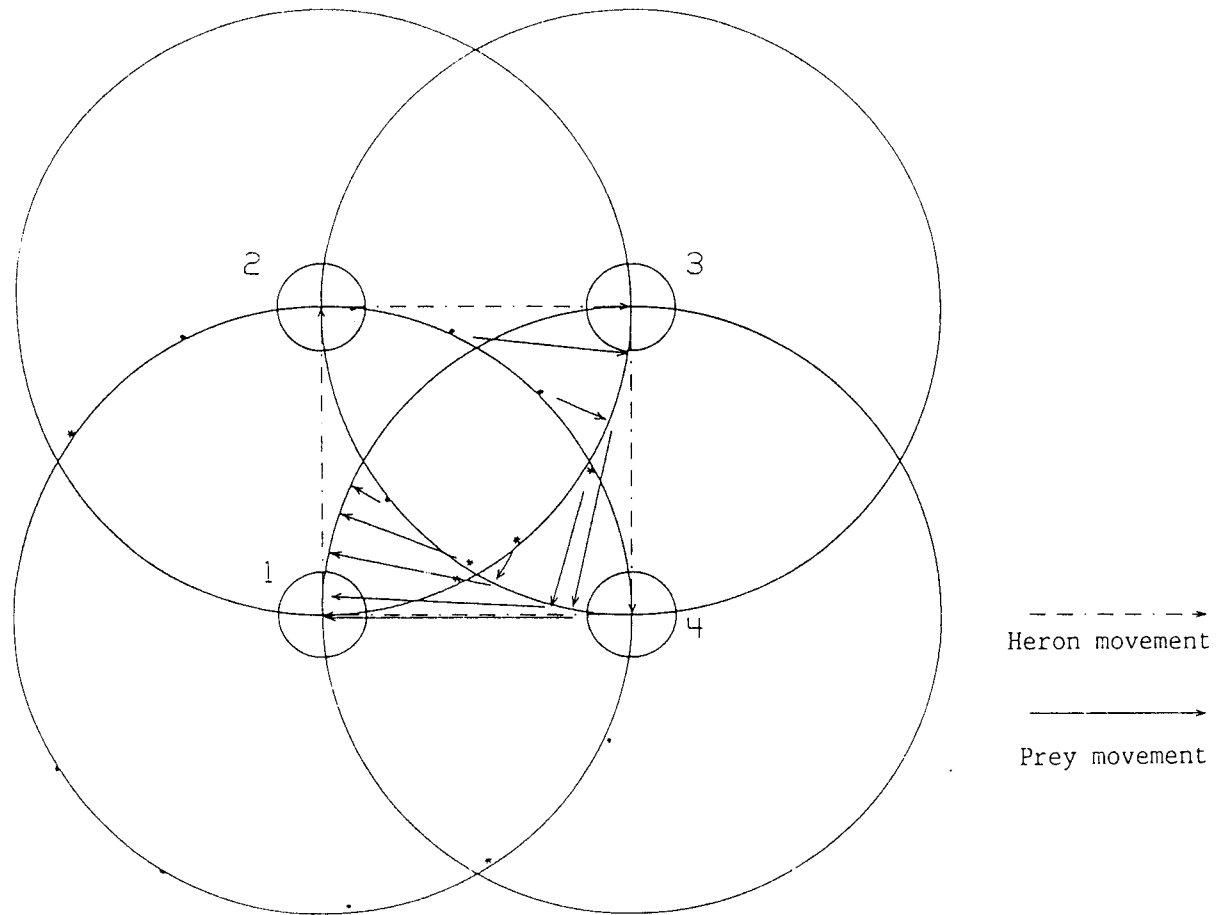
Figure 2. Square search wading bird foraging tactic.

on the prey circles *bc* that the adjacent herons might create by striking (Figures 3 and 4), socially foraging herons could benefit from the increased prey densities on those perimeters. The benefits of foraging in such manner can be quantified; e.g., with a ratio of heron strike radius to prey flight distance of 1:2, a two herons, moving parallel to each other and situated on the perimeter of the prey circle *bc* each would project, could expect to encounter 11% of all remaining prey within the prey circle created by the disturbing heron, in addition to the prey they would normally encounter as they Slow Walked (Appendix). By taking into account prey densities, more specific predictions concerning when it might be optimal to forage in such a manner could be made. For cryptic prey that would otherwise not be detected, this disturbance facilitated foraging might prove particularly effective; disturbed into movement and concentrating on the perimeter of the circles, these prey would be more easily seen and captured. These disturbance facilitated foraging models assume, of course, that herons would learn the appropriate individual distances to keep (the radius of circle *bc*).

Another prey behavior that may select for social foraging is schooling. Re-grouping after a disturbance, schooling prey become a patchy resource may be better kept in sight by a group of foraging herons - on tactical scale, a principle similar to the one describing how patchy
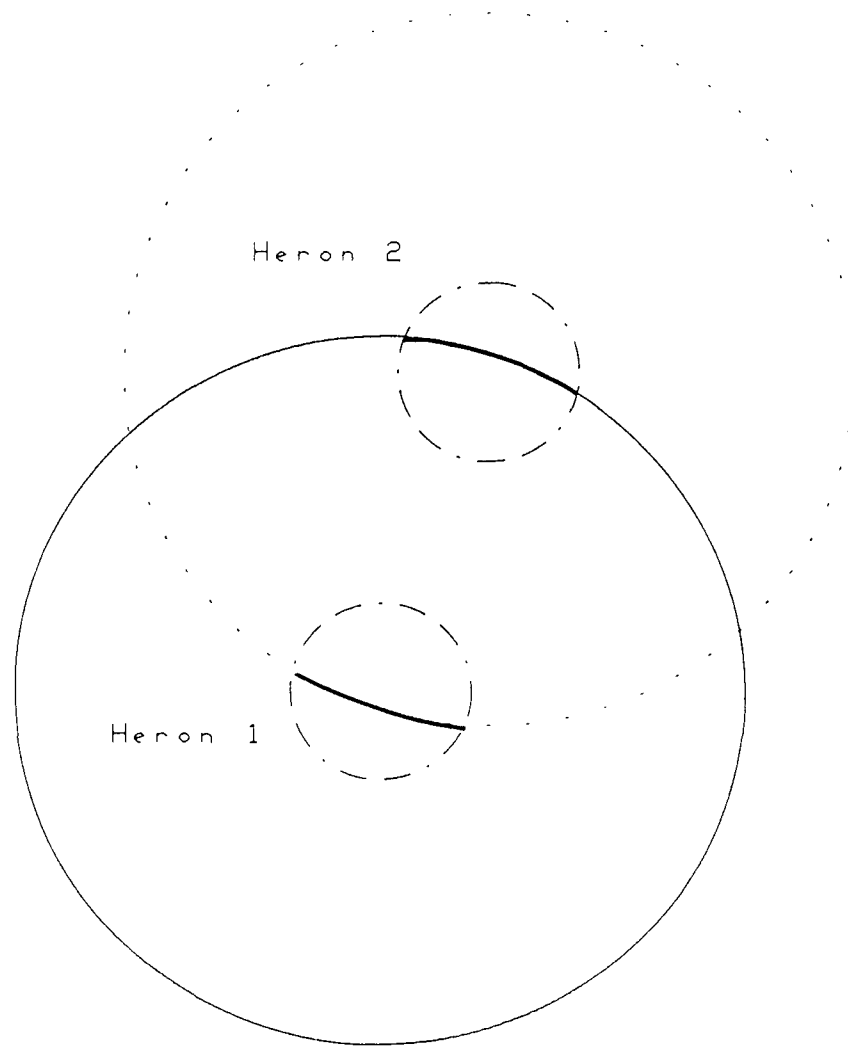
Figure 3. Hypothetical disturbance facilitated foraging by two wading birds.
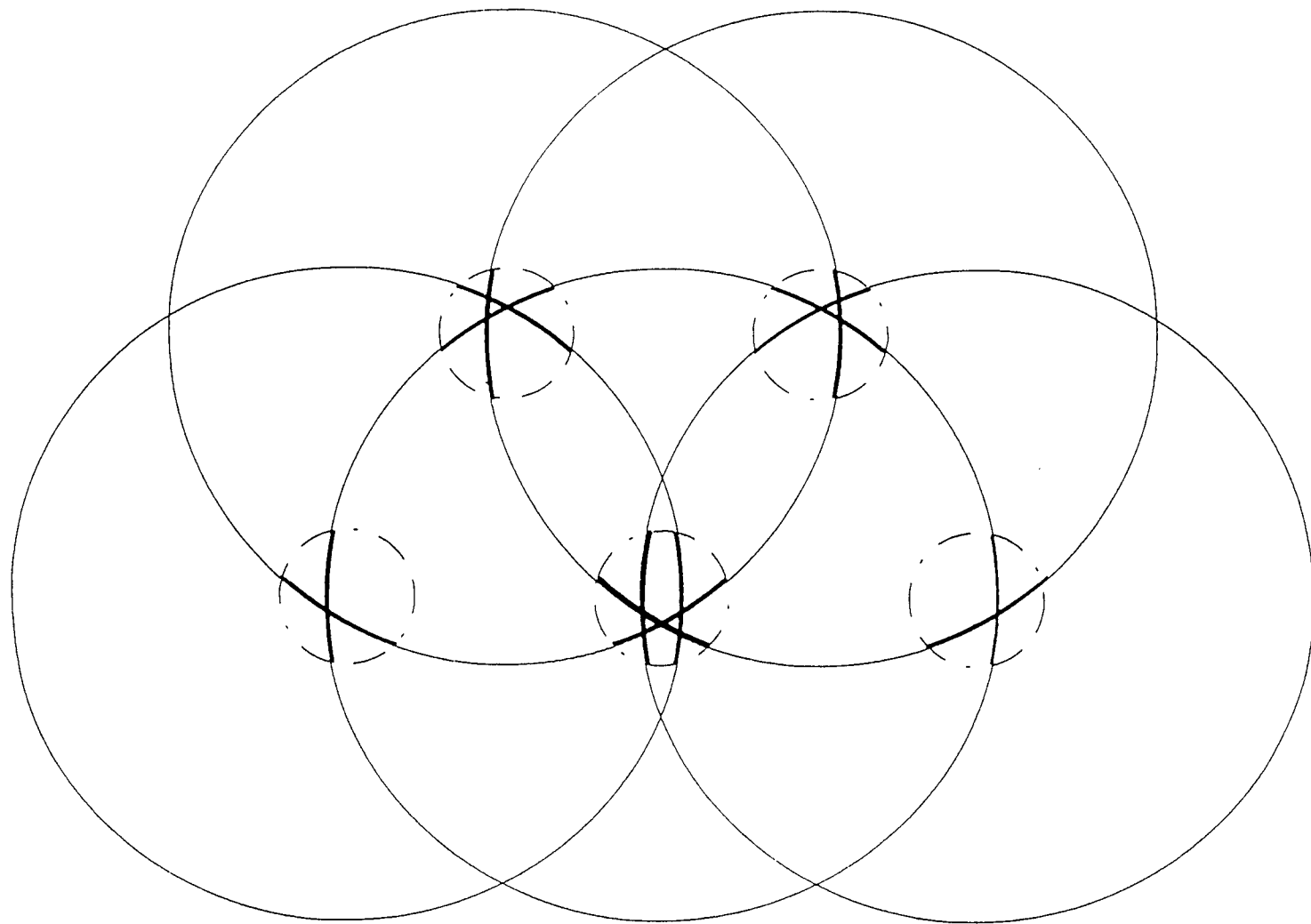
Figure 4. Hypothetical disturbance facilitatated foraging by five wading birds.

resources select for social foraging strategy. Cuing on the strike of an individual, the remaining herons could move to situate themselves on the perimeter of the prey circle, where one would be likely (again, quantifiable given prey flight distances) to contact the re-formed school (Figure 5) Its capture attempt would again cue the remainder of the birds as to the location of the school.

If non-schooling prey flight behaviors in response to wading bird disturbances did not conform to the bomb crater model, the lack of predictable increases in their densities along the perimeter of the disturbance circle would eliminate the increase in foraging efficiency, and disturbance facilitated foraging would then, by definition, be precluded. With the benefits of social foraging thus eliminated, foraging strategy of wading birds would then be determined by prey distribution and density, i.e., evenly distributed prey of intermediate abundances would drive predators toward territoriality and solitary foraging (reviewed Meyers et al. 1981).

A remaining aspect of prey behavior that could select for solitary foraging is the possibility that numerous wading birds in close proximity could drive prey from a foraging area or into refuges. For example, prey adept at predator avoidance, after experiencing multiple threatening stimuli, may move to water too deep for wading birds. This depletion effect may be a severe one, as the energetic cost
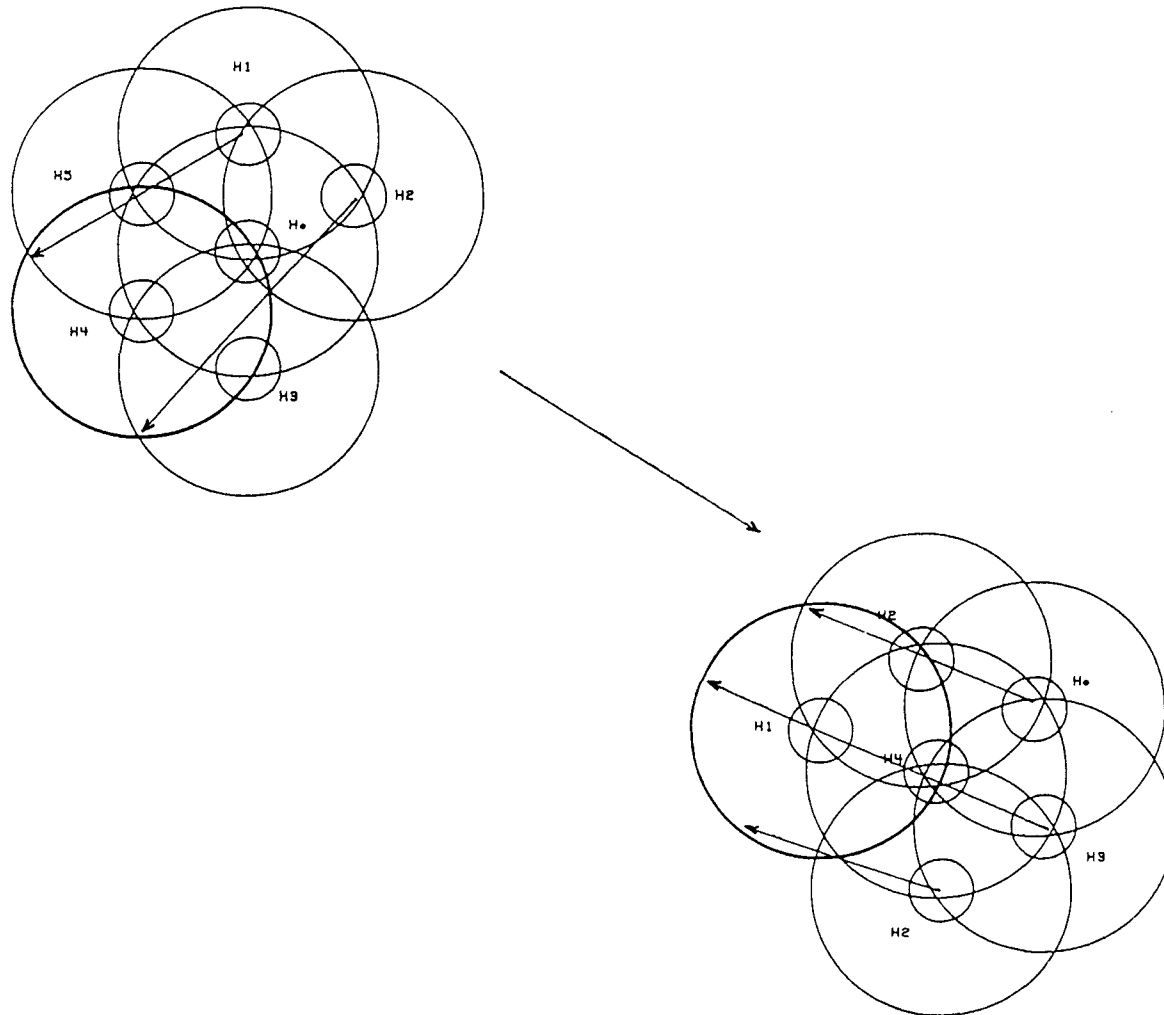
Figure 5. Cuing facilitated foraging by wading birds foraging for schooling prey.

of Slow Walking a short distance to potential prey may relatively minor when compared to that of flying a greater distance to an entirely new area.

In summary, the geometric model bomb crater predicts that prey exhibiting flight responses strongly negatively correlated to a greater disturbance distance would be susceptible to disturbance facilitated foraging and might select for social foraging in wading birds. Likewise, strongly schooling fish could select for social foraging, as numerous wading birds could better remain in contact with the school - similar in principle to the way in which patchy resources♦are thought to select for social foraging strategy. Conversely, non-schooling prey not showing a predictable correlation between flight response and disturbance distance would be unlikely to submit to disturbance facilitated foraging. This lack of increased efficiency by social foragers would not necessarily select for solitary foraging; if, however, social foraging efficiency was reduced to below that of a solitary forager due to prey avoidance behaviors depleting the local resource, solitary foraging strategy would be favored.

CHAPTER III

IMPORTANT FISH PREY OF GREAT BLUE HERONS (<u>Ardea</u> <u>herodias</u>)
FORAGING IN THE COOS BAY ESTUARY

Material and Methods

Great Blue Herons were observed foraging in the
intertidal in three areas: Sitka dock, Haynes Inlet, and
North Slough (Figure 6). All areas are from 0.0 meters (m)
mean lower low water (MLLW) to +1.5 m in elevation, and most
heron foraging observed occurred during the two to three
hours before and one hour after low tide. Within the study
area the endemic eelgrass <u>Zostera</u> <u>marina</u> occurs in varying
densities; also present is the smaller introduced eelgrass
<u>Zostera</u> <u>japonica</u>, though it is present only in the higher
tidal elevations (+1.0 m to + 2.0 m). Using a 20x50
spotting scope, determinations of prey species and size,
using heron bills for scale, were made when herons were
located less than 300 m from observation stations.
Observations were recorded on audio tapes from July through
November 1990 July for a total of 125 hours of observations.
Twenty-four days produced data on heron foraging, with 97
solitary and 105 social foraging bouts observed. A bout was
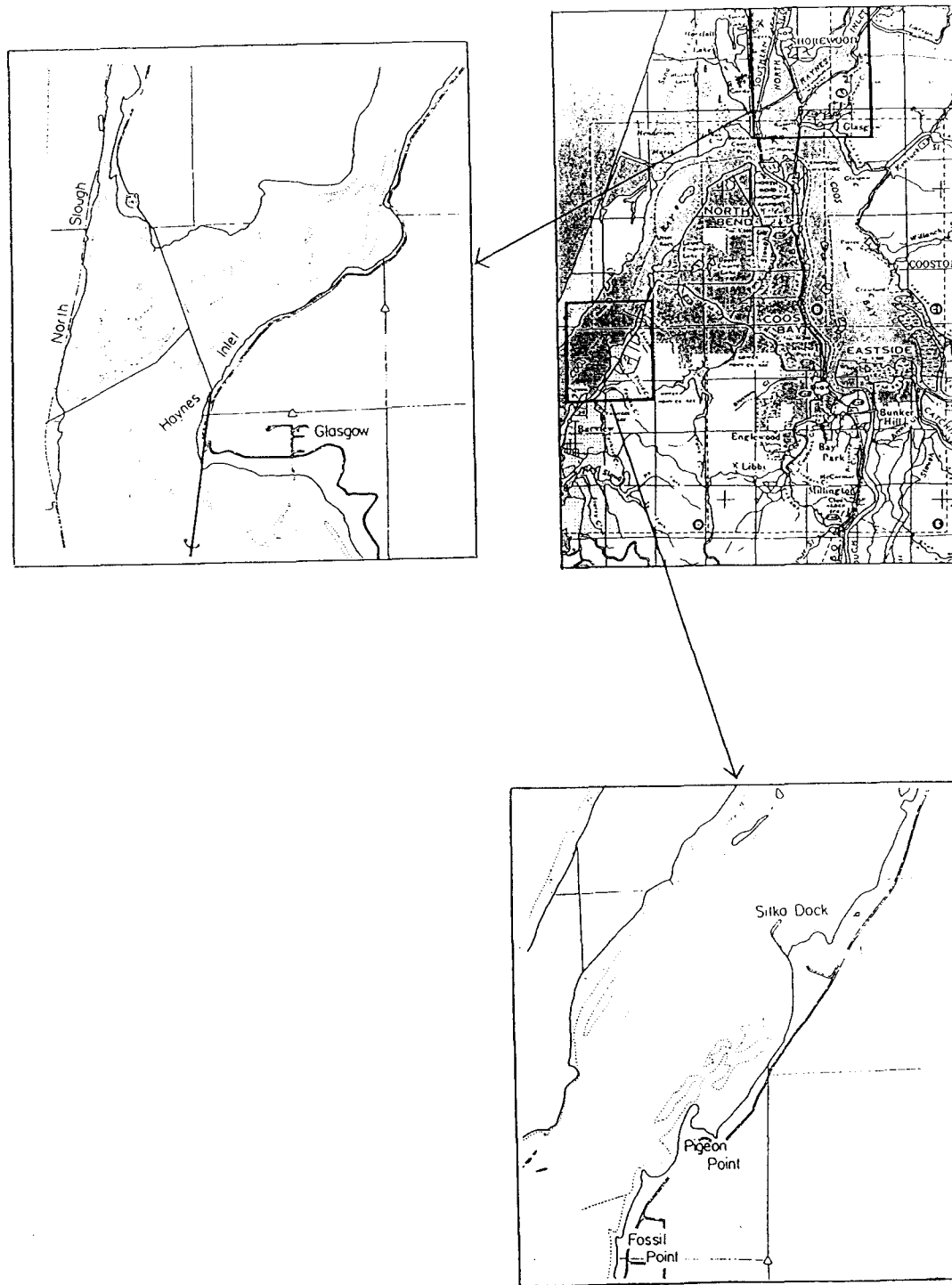
Figure 6. Coos Bay Estuary study sites.

considered to be any foraging event uninterrupted by flights of more than 20 m or movement by any means to a distinctly new foraging area. Socially foraging herons were deemed those herons (and/or egrets, see below) spaced less than 20 m apart and showing no stereotyped territorial behaviors, such as the Upright or Spread-wing postures (Bayer 1984) or other agonistic behaviors that displaced neighboring herons from the foraging area. It should be noted here that not all solitary herons were necessarily territorial, as not all solitary herons observed had the occasion to react to the presence of another heron and behave territorially. No attempt was made to identify individuals beyond the length of a single feeding bout, though solitary herons observed routinely visiting and actively defending the same areas were in all probability the same individuals, as was described by Marion (1989) in the case of the Grey Heron (<u>Ardea</u> <u>cinerea</u>).

Great Egrets (<u>Casmeroidius</u> <u>albus</u>) also forage intertidally in the Coos Bay estuary from April to December. Egrets also forage both solitarily and socially, and in the case of the latter, often in association with Great Blue Herons. As a comparison of their social and solitary feeding habits with those of Great Blue Herons might prove illuminating, their foraging activities were observed and recorded as time permitted.

Results

Though 80% of fish prey were identified to species, some closely related species were grouped for analysis. The Shiner Surfperch (Cymatogaster aggregata), Pile Surfperch (Damalicthys vacca), were grouped by their family Embiotocidae, with the Shiner Surfperch composing (90+%) the bulk of the identified surfperch preyed upon by herons. All flatfish prey were lumped into the order Pleuronectiformes, with the Starry Flounder (Platichthys stellatus) the most common of the identified flatfish (95%). Other flatfish preyed upon were the English sole (Parophrys vetulus) and the Speckled sanddab (Citharicthys stigmaeus. Of the Pholidae and other eel-like fishes, the Saddleback Gunnel (Pholis ornata) was the only identified to species. Herons also took small unidentified prey by casual surface pecking; some were identified as shrimplike crustaceans (either Crangon or Heptacarpus spp.), others as smelt-like fish, possibly juvenile Surf Smelt (Hypomesus pretiosus). The Bay Pipefish (Syngnathus leptorhynchus) was a common prey item of herons foraging in eelgrass beds. The final major component of the observed heron forage was juvenile Lingcod (Ophidon elongatus).

Using personal data and those of Lacerte (1972) and Sanders (1981), length of prey was used to calculate mass, producing the relative contribution of each species to the

heron's diet (Figure 7). With the exception of the unidentified cod, these data are consistent with those of Krebs (1974) who found Staghorn Sculpins, Starry Flounders, and Shiner Surfperch to be the most commonly taken fish species of Great Blue Herons in the estuarine regions of the Fraser River, British Columbia. For herons in the Coos Bay estuary, these four prey species plus the pholids represent over 95% of the fish biomass taken by herons. The observed forage of solitary and social herons are shown in Figures 8 and 9. These data are of limited use for comparing the social and solitary strategies without considering effort (next section), but they illustrate some interesting points. For example, the disparity in the number of gunnels taken by solitary vs. social herons is largely a product of 24 herons feeding in the Sitka Dock site on two consecutive days on or about a 0.0 tide level. On these two respective days, 57 and 90 gunnels were taken by closely (average individual distance < 2-3 meters) grouped herons hunting in water 30-50 cm deep in a dense Zostera marina bed. Also of interest is the complete absence of Flatfishes from the diet of social herons.

Great Egret diet was also dominated (> 95%) by Lingcod, Staghorn Sculpins, Surfperch and Flatfish (Figure 10).

Pleuronectiformes, esp.

Platichthys stellatus

(14.8%)

Leptocottus armatus

(28.2%)

Syngnathus leptorhynchus

(2.3%)

(14.1%)

Embiotocids, esp.

Cymatogaster aggregata

Pholids, esp Pholis ornata

(13.9%)

(24.7%)

(1.9%)

Ophidon elongatus

Unident. small, esp. Crangon and
Heptacarpus
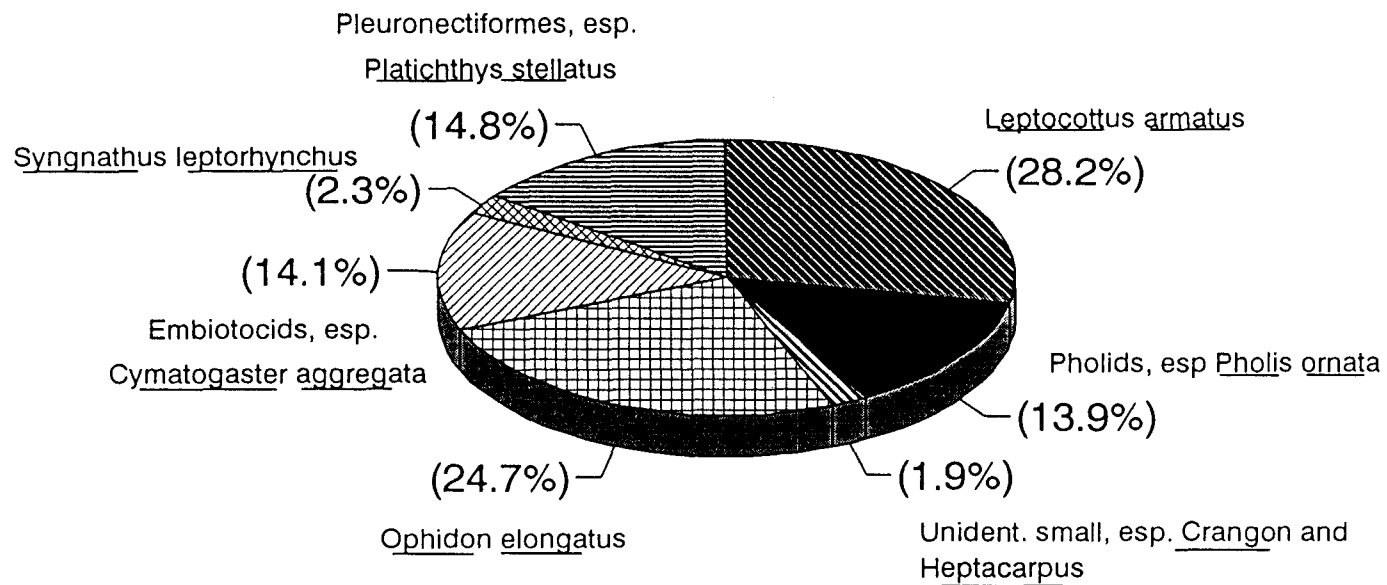
Figure 7. Great Blue Heron observed forage by wet weight.
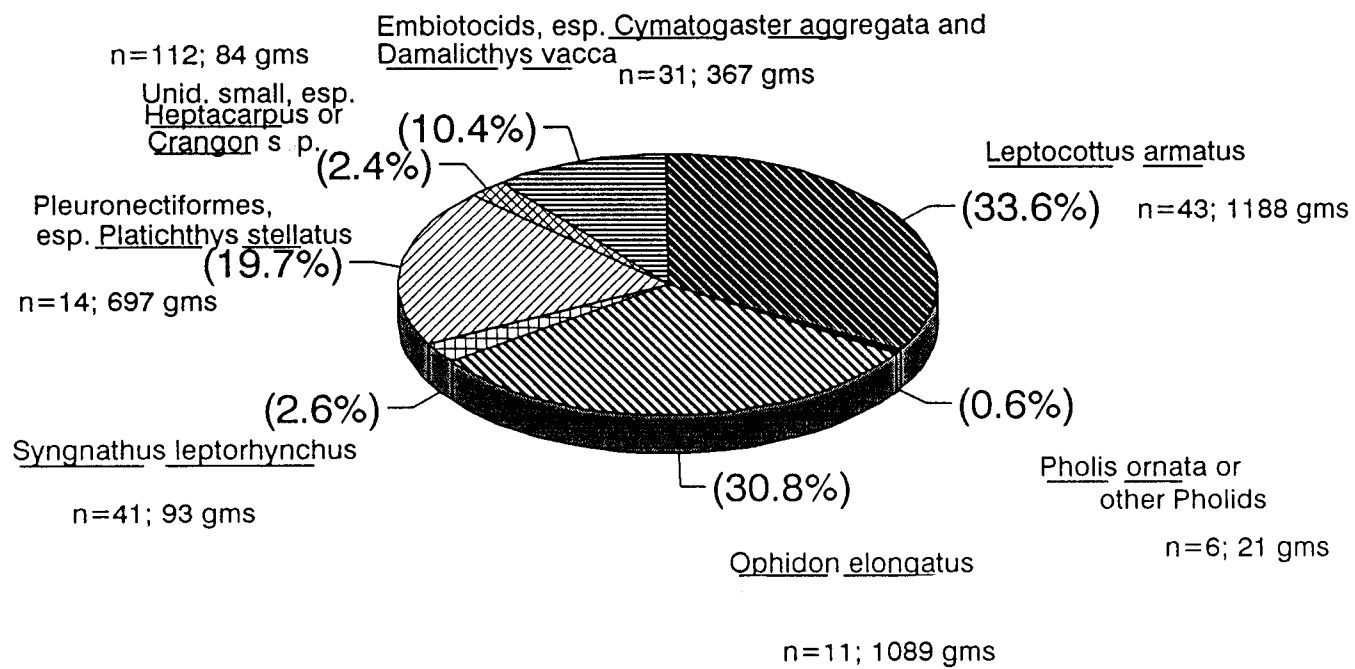
Figure 8. Solitary Great Blue Heron observed forage by wet weight.

Sygnathus leptorhynchus
n=7; 77 gms
(1.4%)

Leptocottus armatus
n= 7; 144 gms
(12.3%)

(0.6%) Unid. small, esp.
Heptacarpus and Crangon s p.
n=10; 7 gms

Pholis ornata
or other Pholids
(54.0%)
n=159; 636 gms

(25.1%) Embiotocids, esp.
Cymatogaster aggregata
and Damalicthys vacca
n= 50; 296 gms

(6.6%)

Ophidon elongatus

n=1; 77 gms
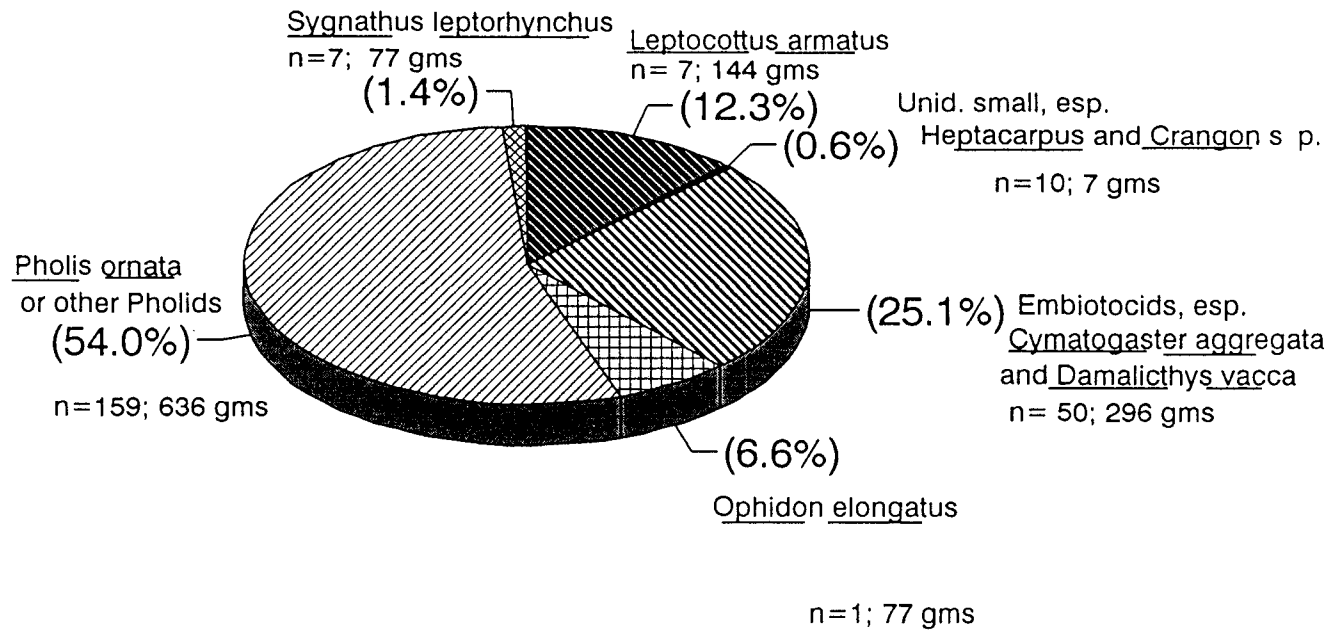
Figure 9.   Social Great Blue Heron observed forage by wet weight.

n=4, 109 gms
Pleuronectiformes, esp.
Platichthys stellatus

Embiotocids, esp. Cymatogaster aggregata

Leptocottus armatus

n=17, 134 gms

n=10, 340 gms (14.3%) (4.6%) (5.6%)

Other

n=19, (1.3%)

31 gms

(74.3%)

Microgadus proximus

n=20, 1771 gms
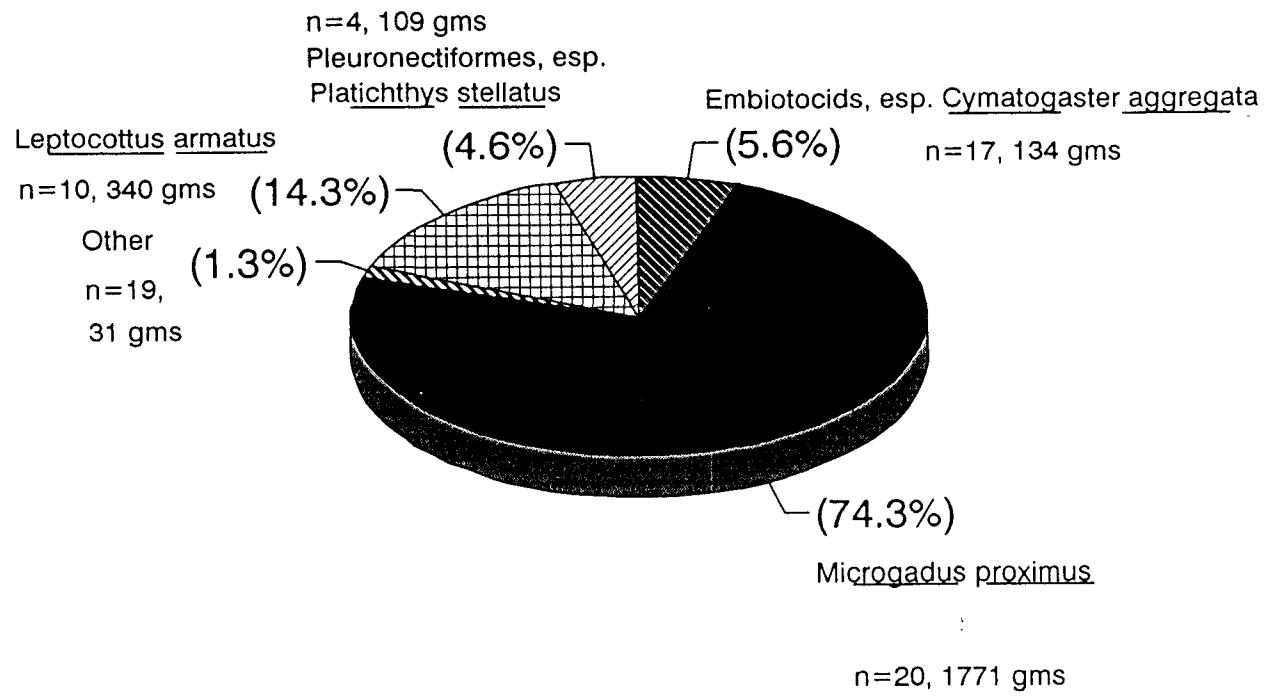
Figure 10. Great Egret observed forage by wet weight.

CHAPTER IV

FORAGING RATES OF GREAT BLUE HERONS

ON IMPORTANT PREY SPECIES

Materials and Methods

Data used in this analysis were collected concurrently
with those used in Chapter III. To reiterate, social
herons, as distinguished from solitary herons, were any
herons less than 20 meters apart displaying no stereotypical
territorial or agonistic behaviors resulting in the
displacement of neighboring herons. The length of a feeding
bout was recorded to the nearest second. In observing
socially foraging birds, entire groups were generally not
watched; rather, random individuals (or subgroups, if the
spotting scope field of view allowed) within the flock were
watched for a time interval appropriate to the dynamics of
the group. For example, for a loose, mobile aggregation,
individuals were watched until they moved purposefully
(often short flights) and out of the field of view. More
sedentary groups allowed for longer observations on the
selected individuals (or subgroups) within the group. As
keeping track of individuals was essential, observed

subgroups were limited to a maximum of three or four birds. To control for the possible effects of prey depletion during a foraging bout, only herons near the beginning of a bout were observed.

Results

Individuals from 11 aggregations of socially foraging Great Blue Herons were observed; the number of individuals per aggregation ranged from 2 to 31. Solitary Great Blue Herons were observed foraging on 93 separate occasions, for a total of 34.2 bout hours, with a mean foraging bout length of 22.0 minutes. The "square search" tactic, predicted as an effective tactic for concentrating prey whose flight responses conform to the bomb crater hypothesis, was not seen in any foraging heron or egret. Social Great Blue Herons foraging bouts were observed foraging on 106 separate occasions for a total of 7.4 bout hours and a mean foraging bout time of 4.2 minutes (summarized Table 1). The mean foraging rates (prey/hour) of solitary and social herons and egrets for the 7 primary prey groups are listed in Table 2, and illustrated in Figures 11 and 12. As compared to solitary Great Blue Herons, social Great Blue Herons had significantly higher capture rates of pholids ($t = -2.367$, $P = .02$) and lower capture rates of unidentified small prey ($t = 2.674$, $P < .01$). No flatfish were seen taken by social

Table 1. Observational Effort and Duration of Feeding
Bout, Social and Solitary Great Blue Herons
and Great Egrets

Forager type	n	Total bout hours	Mean bout duration (min)	sd (min)
Solitary Herons	93	48.8	41.2	39.6
Social Herons	106	7.4	4.2	5.3
Solitary Egrets	9	1.8	12.0	15.0
Social Egrets	26	5.1	11.8	13.0

Table 2. Mean Foraging Rates (Prey Captured/Hour) of
Solitary and Social Great Blue Herons, Great Egrets
for Primary Prey Species Groups

Prey species	Great Blue Herons Solitary	Social	Great Egrets Solitary	Social
L. armatus	1.83	0.59	3.67	0.88
Embiotocids	3.30	6.92	2.45	0.85
Pleuro- nectiformes	0.68	0.00	0.40	0.24
Ophidon elongatus	0.25	0.23	1.25	5.64
Pholids	0.24	2.03	0.33	12.75
S. leptorhynchus	1.55	0.57	0.00	0.37
Unid. small	8.20	2.07	0.00	1.96
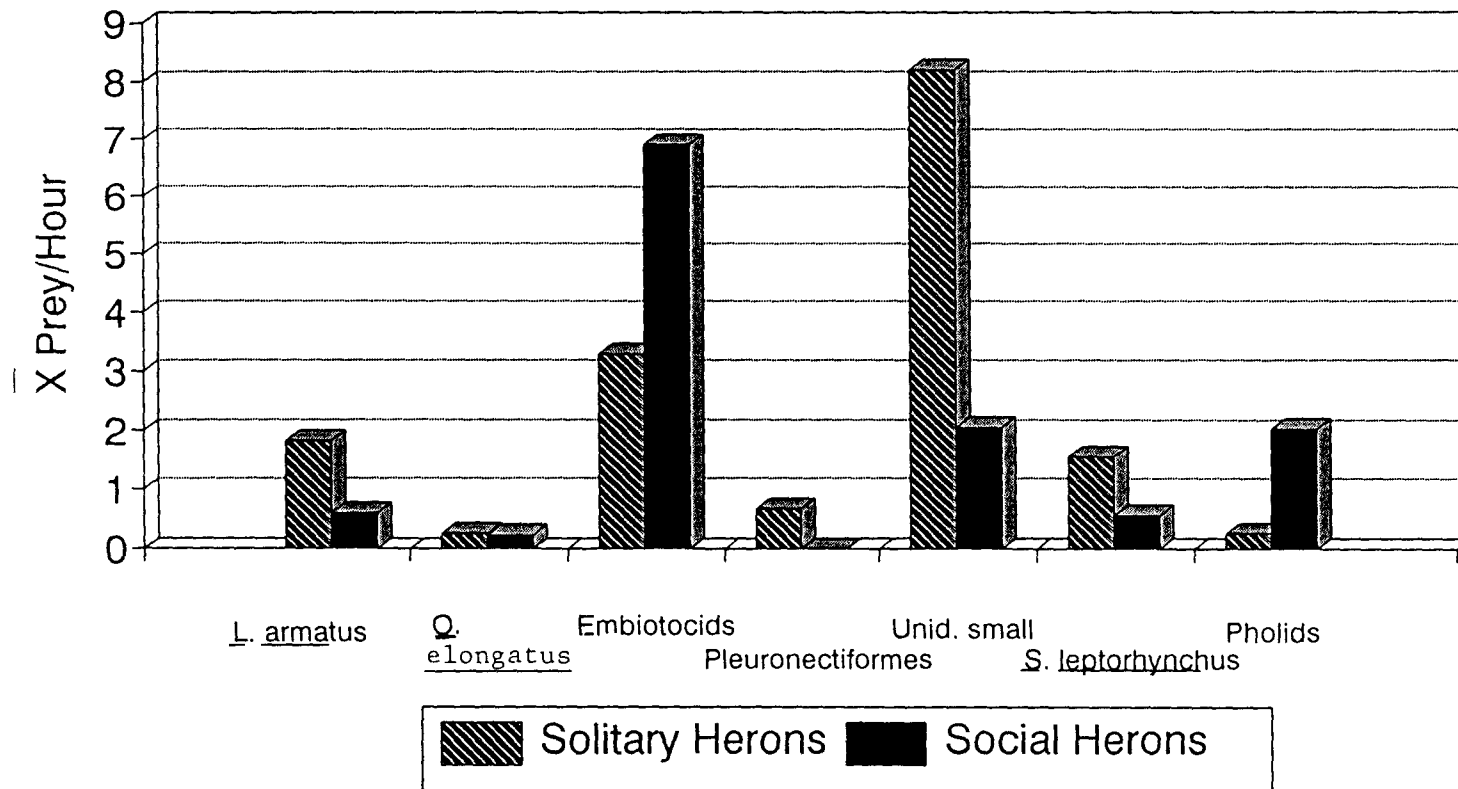
Figure 11. Mean prey/hour, solitary and social Great Blue Herons.
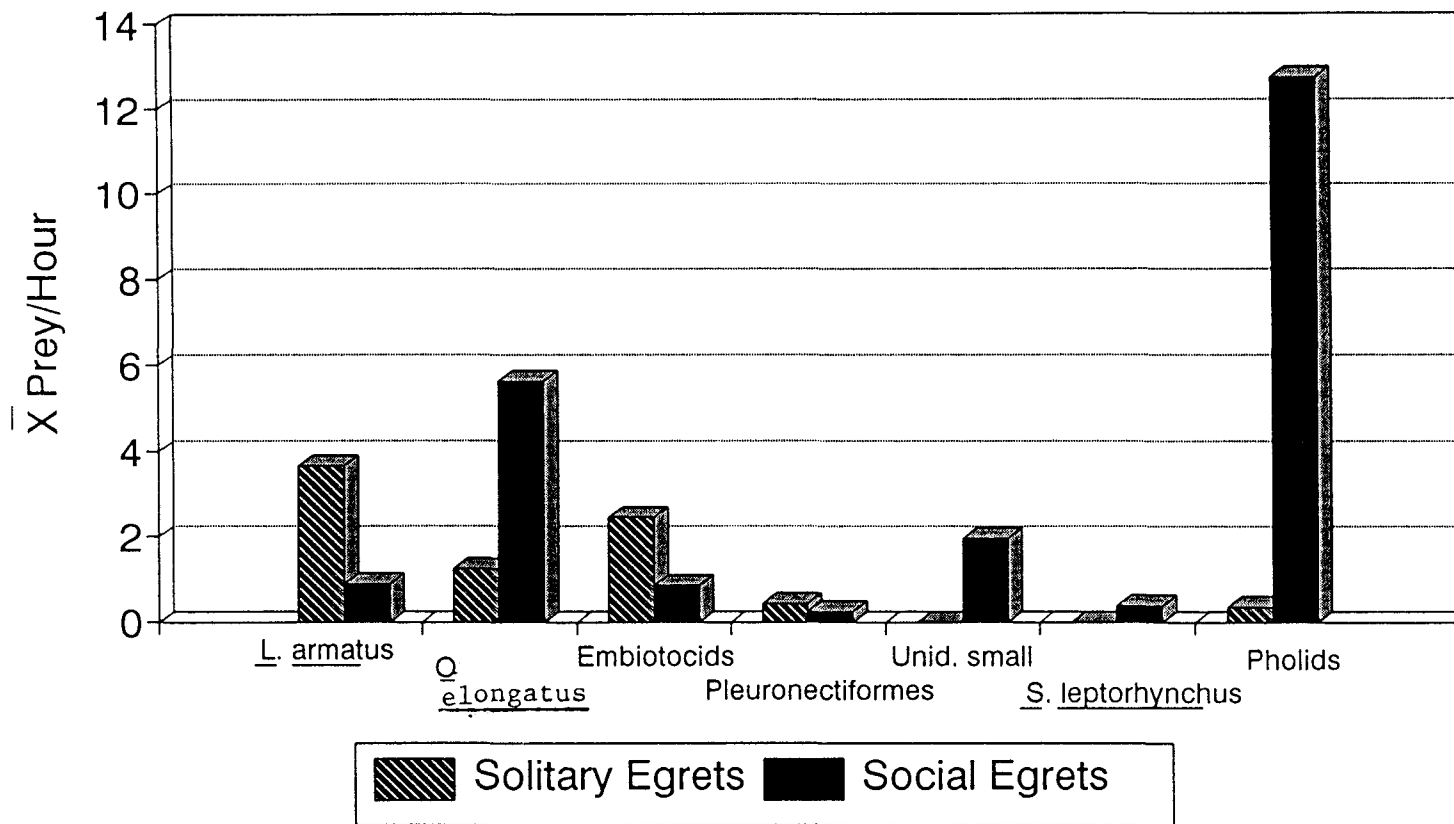
Figure 12. Mean prey/hour, solitary and social Great Egrets.

Great Blue Herons, and Staghorn Sculpins were taken at a significantly lower (t = 2.05, P ≤ .05) rate by social herons (mean = .59, sd = 3.58) than solitary (mean = 1.826, sd = 4.395). The importance of the Staghorn Sculpin as a prey species and the implications of this analysis led to a further investigation of these data. It was found that of the 4 sculpins taken by social herons, 3 were taken by social "groups" composed of two herons. Eliminating these from the data set brought the mean rate for social herons down to .31 sculpins/hr, t = 2.501, P < .02. This effect indicates that an analysis of foraging rates for different prey species regressed against foraging flock size might be an interesting one; unfortunately, there were insufficient data for such an analysis.

The only significant difference in prey species foraging rates for egrets was for pholids (t = -2.650, p = .014).

Discussion

Feeding rates of foraging herons on specific prey may be simply related to the prey abundance in a particular area, as was suggested by Krebs (1974) as an explanation for higher feeding rates seen in socially foraging herons (though in that instance, no mention was made of prey type). In other words, Great Blue Herons may forage socially only

when dense aggregations of prey such as the schooling Shiner Surfperch or other embiotocids make cuing on other foraging herons profitable. Furthermore, once foraging for surfperch, developing a search image for these prey may preclude identifying other prey, particularly the more sedentary and cryptic Staghorn Sculpins and flatfish, that may co-occur in the area (Tinbergen 1960, Alcock 1973). Conversely, the fact that low value food items (mean mass < .5 gm, Appendix B) such as Crangon and Heptacarpus were not taken as frequently by Great Blue Herons within groups as by solitary herons indicates that Great Blue Herons aggregate only to exploit ephemeral abundant high quality prey. Though the data are limited for Great Egrets in this case, they do pose an interesting contrast. Great Egrets, whose highly visible all-white plumage may attract other individuals to a feeding area (Hancock and Kushlan 1984) can be considered a more social species, and as such would be more likely to be observed foraging in groups for any prey, regardless of abundance or quality, thus explaining the many small unidentified prey taken when foraging as a group.

In summary, given the lower social Great Blue Heron and Great Egret bout-hour effort and lack of clear prey trends between and among social and solitary herons and egrets, it is safest to suggest that the differences seen in their foraging were simply a result of exploitation of a patchy resources and/or search image fixation - with two

exceptions.

In both Great Blue Herons and Great Egrets, socially foraging birds had lower catch rates of the Staghorn Sculpin and flatfish. Again, this may be because social groups of birds were concentrating on other ephemeral and more abundant prey. Given, however, the ubiquity and abundance of the Staghorn Sculpin and flatfish (Bayer 1981, Emmett et. al. 1991, pers obs.), it is interesting that solitary birds of both species had higher catch/effort than did socially foraging individuals. Moreover, given sculpin and flatfish abundances one might ask why they were never the specific object of an aggregation of socially foraging herons or egrets. A possible answer is that sculpins and flatfish occurred in those areas occupied by territorial herons and did not in those areas where herons foraged socially. Marion (1989) found that the primarily territorial Grey Heron when foraging socially utilized "neutral" areas that were resource poor, or rich but unpredictable and/or unappropriable. The limited data on area use by social and solitary Coos Bay estuary Great Blue Herons and Great Egrets implied no such phenomenon. Of the 11 aggregations of Great Blue Herons observed, 4 were foraging in eelgrass beds - 2 of which were later occupied by a territorial heron (that was later observed taking sculpins). Furthermore, social Great Egrets were often observed foraging in the same high quality territories held by Great Blue Herons - often

concurrently. (In these latter cases, Great Egrets may have been tolerated only due to the fact that the standard territorial postures employed by the herons were *non sequiturs* to the intruding egrets, and were ignored.) Moreover, data collected by Bayer (1981) indicate that the Staghorn Sculpins may be equally abundant on unvegetated mudflats as in eelgrass (<u>Zostera</u> <u>marina</u>). It would thus seem entirely likely that Staghorn Sculpins are often found in the areas where socially foraging wading birds were seen.

In summary, foraging data collected on Great Blue Herons and Great Egrets in the Coos Estuary may in large part simply reflect social foraging groups taking advantage of rich but patchy and ephemeral prey abundances. Without knowing precisely which and how many of a prey species are in a location at the time of foraging, speculation on the influence of the reactive behaviors of those prey would not be appropriate. The case of the Staghorn Sculpin, however, poses an interesting question. In the following section, this species, due to its general importance as prey, ubiquitous distribution in varying estuarine habitats, and apparent resistance to capture by socially foraging wading birds, has been selected for a study of its reactive behaviors. For contrast, the Shiner Surfperch, also shown to be an important prey species, and one that seems much more susceptible to predation by socially foraging herons and egrets, was also studied.

CHAPTER V

THE FLIGHT RESPONSES OF HERON PREY SPECIES (STAGHORN

SCULPINS AND SHINER SURFPERCH) TO SIMULATED

WADING BIRD DISTURBANCES

<u>Materials and Methods</u>

Physical Characteristics of the Experimental
Environment

Disturbance experiments were performed at the

University of Oregon Institute of Marine Biology, located

near the harbor entrance of Coos Bay. A wood framed,

10m x5m x.5m tank was constructed within a semi-enclosed

room equipped with running seawater. The concrete floor of

the tank room served as the floor of the tank, and two

layers of 6 mil translucent polyethylene plastic lined the

tank. The bottom of the tank was covered with 3 cm of 70

grit (0.2 mm, Wentworth fine sand) white silica, simulating

the natural substrate of benthic fish in the Coos Bay

estuary (personal obs.). Naturally occurring substrates

were not used as they were deemed too dark to allow for

precise observation of subjects, whereas the combination of

white sand atop translucent plastic over the white concrete

floor created the greatest possible contrast between substrate and subject, thus enhancing observability. Flat (1 cm thick), circular (3 cm diameter) lead weights, painted red and coated to prevent lead leaching, were placed on the white substrate at 1 m intervals to provide scale for assessing prey movements. Seawater taken directly from the bay was run continually through the tank; temperatures ranged from $10-12°$ C, and salinities from 30-32 ppt., both well within the tolerances of these euryhaline species (Emmett et al. 1991). Water depth for the experiment was 35 cm, close to the maximum depth in which a heron could forage (pers. obs.). The perimeter of the tank was surrounded by black polyethylene plastic to eliminate outside disturbances. The observer was located 3 m directly above the tank in a blind constructed in the rafters of the tank room; access to the blind was clandestine from behind the black plastic curtain. From here, a prone observer had unobstructed (though at times inverted) view of the entire tank, and disturbances could be created and controlled remotely by the observer. Video cameras located 2 m above and at either end of the tank were used to facilitate data collection.

Simulating the Heron Disturbance

The strike was chosen as the primary disturbance to

simulate. The rationale for the assumption that the strike is the greatest disturbance created by a foraging heron has already been discussed; summarized, if wading birds were consistently seen by prey before they struck, the birds would never be successful. Moreover, given that the conditions in the experimental tank had been optimized for clear viewing, they would also create a more visual environment than the more turbid estuarine waters the fish normally occupy. Thus, the "strike only" disturbance would minimize the potential for any supernormal stimuli. Finally, presenting both an image of a heron and simultaneously producing a realistic simulation of a strike was deemed prohibitively difficult, given the prey mobility allowed by the large tank.

Using museum specimens of Great Blue Herons as a standard, 25cm x4cm x4cm blocks of clear fir were tapered to 1.5cm x 0.5 cm, resulting in a shape emulating the head and bill, and a mass of 105 $\pm$ 5 g. The "heads" were painted black that against the black plastic background surrounding the tank they would present a minimal visual stimulus as lowered. Thirteen such identical heads were suspended via light line and pulleys at equal intervals above the tank (Figure 13). The heads remained retracted and hidden in the rafters until used. The lines suspending each head terminated in the observer blind; when the observer wished to create a disturbance, the heads were lowered slowly to
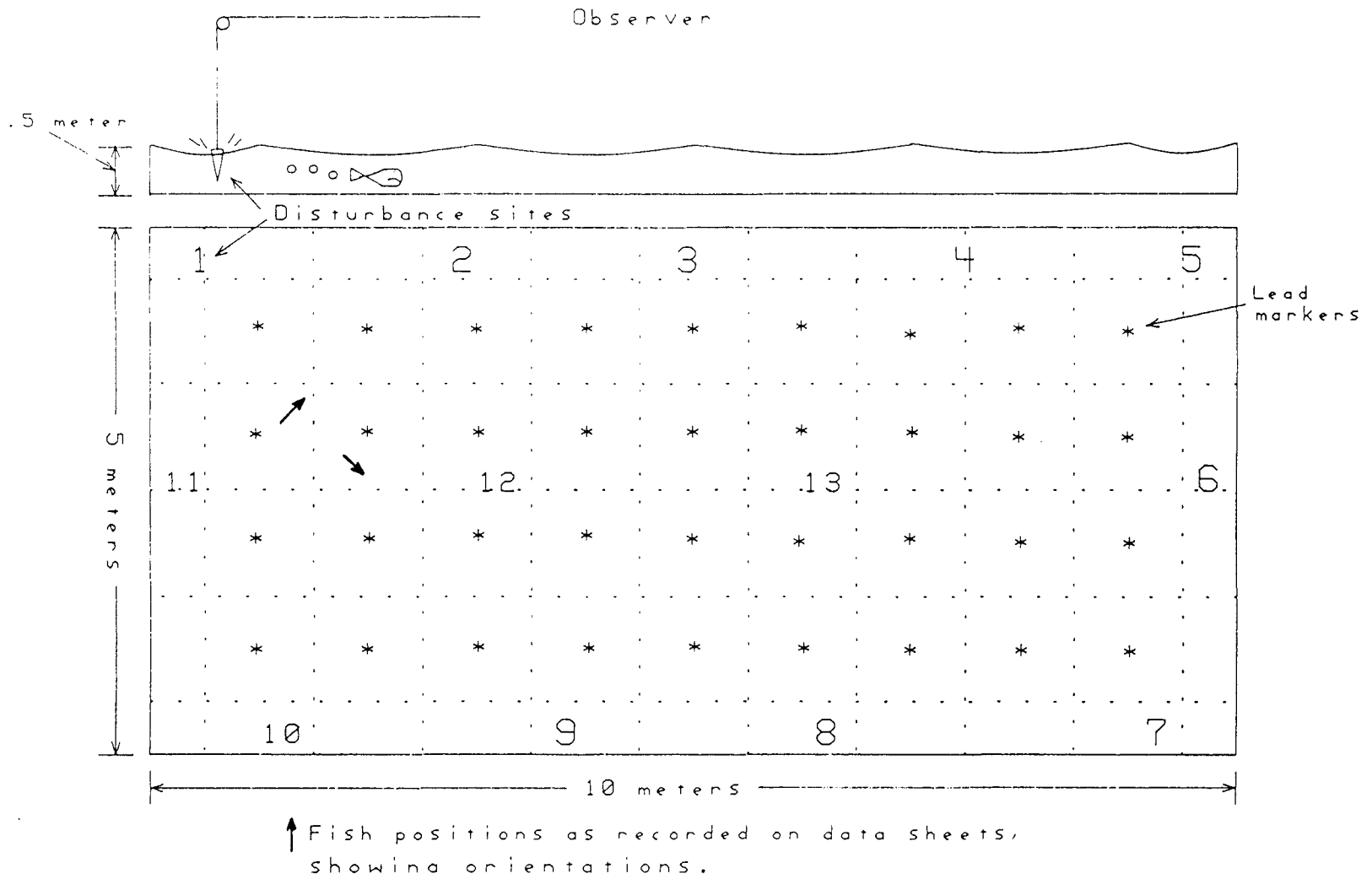
Figure 13. Prey flight response experimental environment and data sheet.

within 66 cm of the water's surface and then released. The
energy of the head falling from this height and the
disturbance it created was estimated to be comparable to
that created by a striking heron. Each suspension line
terminated at the observer's end with a cork stopper. The
procedure to create a uniform strike was to line up the cork
on a point 1 meter from a small eye bolt through which the
suspension line passed. When released, the head would free-
fall precisely that 1 m until arrested by the cork impacting
the eye. The strike thus penetrated 34 cm into the water,
stopping 1 cm short of the bottom of the tank, thereby
avoiding a "wood-on-concrete" sound not normally experienced
by heron prey. The heads were immediately and quickly
retracted to their hiding places in the rafters after the
drop.

Disturbance experiments were generally conducted once
every 25 hours for 1.5 to 2 hours, roughly duplicating the
tidal cycle and the prey's resulting exposure to heron
predation. To reduce the possibility of habituation, no
more than 10 disturbances were performed in any session.

After some experimentation on Staghorn Sculpins
(performed after the experiments with Shiner Surfperch),
concern grew that the heads were not a powerful enough or
appropriate stimulus. Therefore, some experiments using
images of Great Blue Herons were performed with Staghorn
Sculpins. Plastic likenesses of Great Blue Herons,

realistic enough to fool keen-eyed and wary ducks (duck hunter's "confidence decoys" Cabelas, Fall 1989) were suspended from 5 of the same lines used for strike disturbances. For these tests, the image was simply lowered steadily and gently into the water until it "stood" on the bottom. The image remained in the water for 1 minute, or until all prey reactions had ceased.

Data Recording

All the data recorded for Shiner Surfperch were taken from video tape recordings of the disturbances experiments. Not being a particularly cryptic fish, and as the white sand substrate was yet fairly pristine, video resolution was more than adequate for observation of the entire school.

The cryptic nature of Staghorn Sculpins and the gradual siltation and darkening of the white substrate precluded use of video cameras for recording their behaviors. Data on their movements were instead recorded on a scale data sheet representation of the experimental tank, which included the lead-weight marker positions. Using the 1 m squares marked by the lead weights, flight behaviors were interpolated to the nearest 25 cm. Binoculars were often employed by the observer to find and identify individuals; this technique, though somewhat effective, limited the field of vision and plasticity of the observer. Thus, individuals were

generally not identified and followed for more than one disturbance. Three size categories of Staghorn Sculpins were distinguished: Small (< 8.5 cm), medium (8.6 - 10.1 cm), and large (11 - 14 cm). The orientation (the continuum from facing toward to facing directly away) of each fish was recorded prior to after the disturbance (Figure 13), and was later quantified for analysis.

Capture and Care of Fish

Fish used in the behavioral experiments were captured and held per the approval of the University of Oregon Animal Care and Use Committee, Application # 018-91, Assurance # A-3009-01; and Oregon Department of Fish and Wildlife Scientific Taking Permit # 1-1263.

Shiner Surfperch were captured with a 20 meter, pursed beach seine; all 171 used in the study were taken in one 30 meter pull through a sparse eelgrass bed north of Sitka Dock on 23 May, 1991. The fish were immediately transferred to the study tank and left to acclimate for one week before experiments were commenced. One mortality occurred, presumably from the stress of capture, within 24 hours of introduction into the tank. From the blind, fish were fed pellet fish food daily. Studies of surfperch behaviors began on 30 May, 1991 and ended 33 days later, at which time they were released into the estuary.

Staghorn Sculpins used in the second part of the study were captured with a 20 m pursed beach seine from mudflats near Sitka dock. Five individuals of each of the size classes were captured on 15 July 1991 and immediately transferred to the study tank, with two mortalities, one medium and one small, occurring within 24 hours. Once daily Staghorn Sculpins were fed live Callianassa californiensis, a burrowing shrimp of the tideflats and natural prey of Staghorn Sculpins (Posey 1986), which were purchased at a local bait shop. Experiments concluded 40 days later, at which time the sculpins were returned to the estuary.

Results

The Flight Responses of the Shiner Surfperch (Cymatogaster aggregata)

As Shiner Surfperch, henceforth referred to as "surfperch," is not a sedentary, benthic species, and are therefore not inclined to exhibit flight responses with clearly defined starting and stopping points, flight response distances were described in terms of three observed speed of movement categories (Figure 14): Type 3, the initial evasive burst (1.75 - 2.5 m/sec); type 2, the general flight speed (1 - 1.5 m/sec), which typified speed individuals used in reforming the school after a scattering disturbance; type 1, (< .5 m/sec), the speed commonly exhibited by the school as it moved away from the general
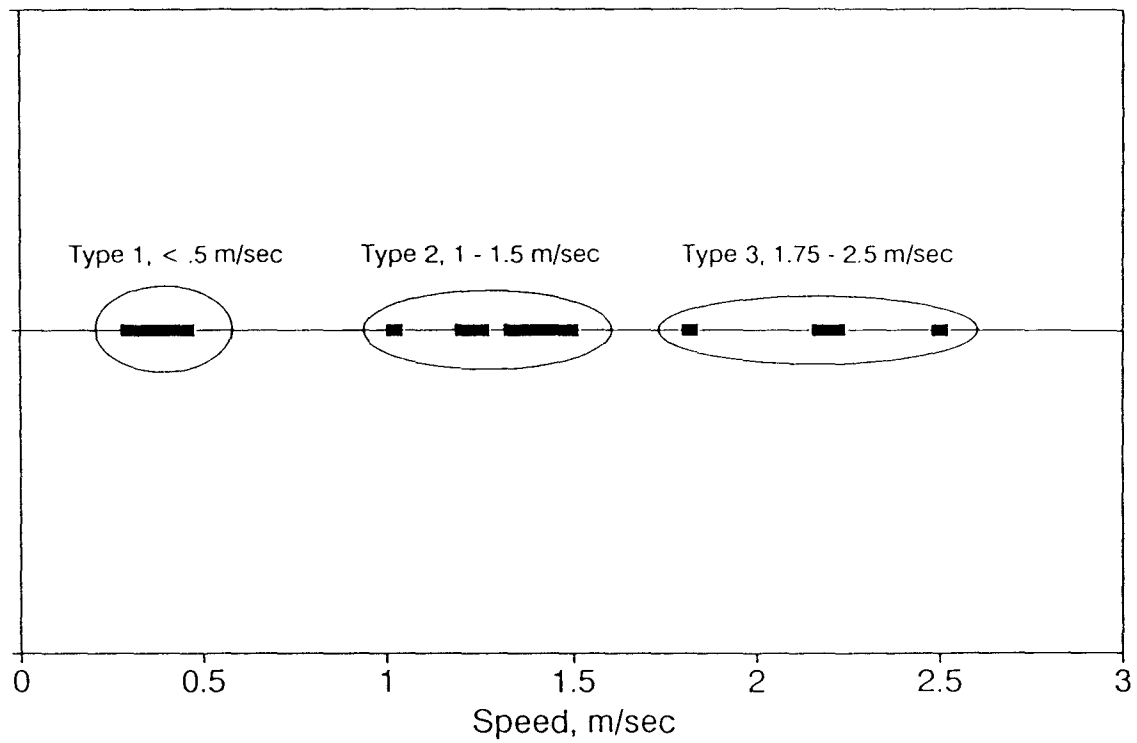
Figure 14. Surfperch speed of movement in response to disturbance.

area of the disturbance.

Surfperch are a schooling fish (Bane and Robinson, 1970, Emmett et. al. 1991) and any discussion of their flight behaviors must be within this context. For the sake of applying their responses to the geometric model, however, it was necessary to analyze their responses as individuals within the school. This analysis, performed on only first disturbances of the session, shows the initial flight distance, as defined by the type 3 evasive burst speed, of individuals to a disturbance before individuals re-submitted to schooling behavior. The flight responses of individuals vs. disturbance distance is shown in Figure 15; a regression analysis describes the relationship of these variables as FD = -.30DD + 1.14, where FD = Flight Distance and DD = disturbance distance, ($n = 61$, $r^2 = .43$, standard error of y estimate .36, x coefficient $t = -6.65$ and $p < .001$). The threshold of response with a type 1 evasive burst to a strike stimulus was 3.75 meters. Figure 16 illustrates the result of these responses. The loose schooling of the fish prior to any disturbances is probably a good approximation of the natural "relaxed" state of the fish as they forage for prey such as crab megalopae (Emmett et. al. 1991, pers. obs.), other zooplankton and small benthic crustaceans. After the disturbance and the individual responses creating the ephemeral distribution very similar to the circle *bc* predicted by the geometric model, the school reforms (<10
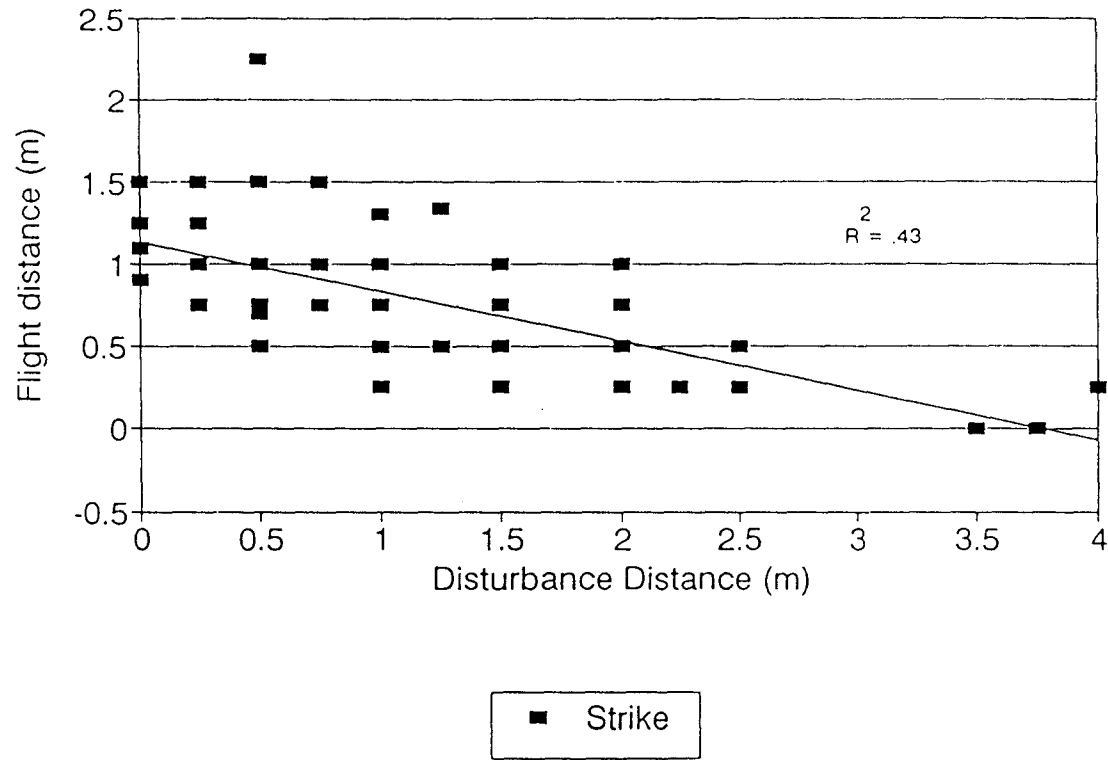
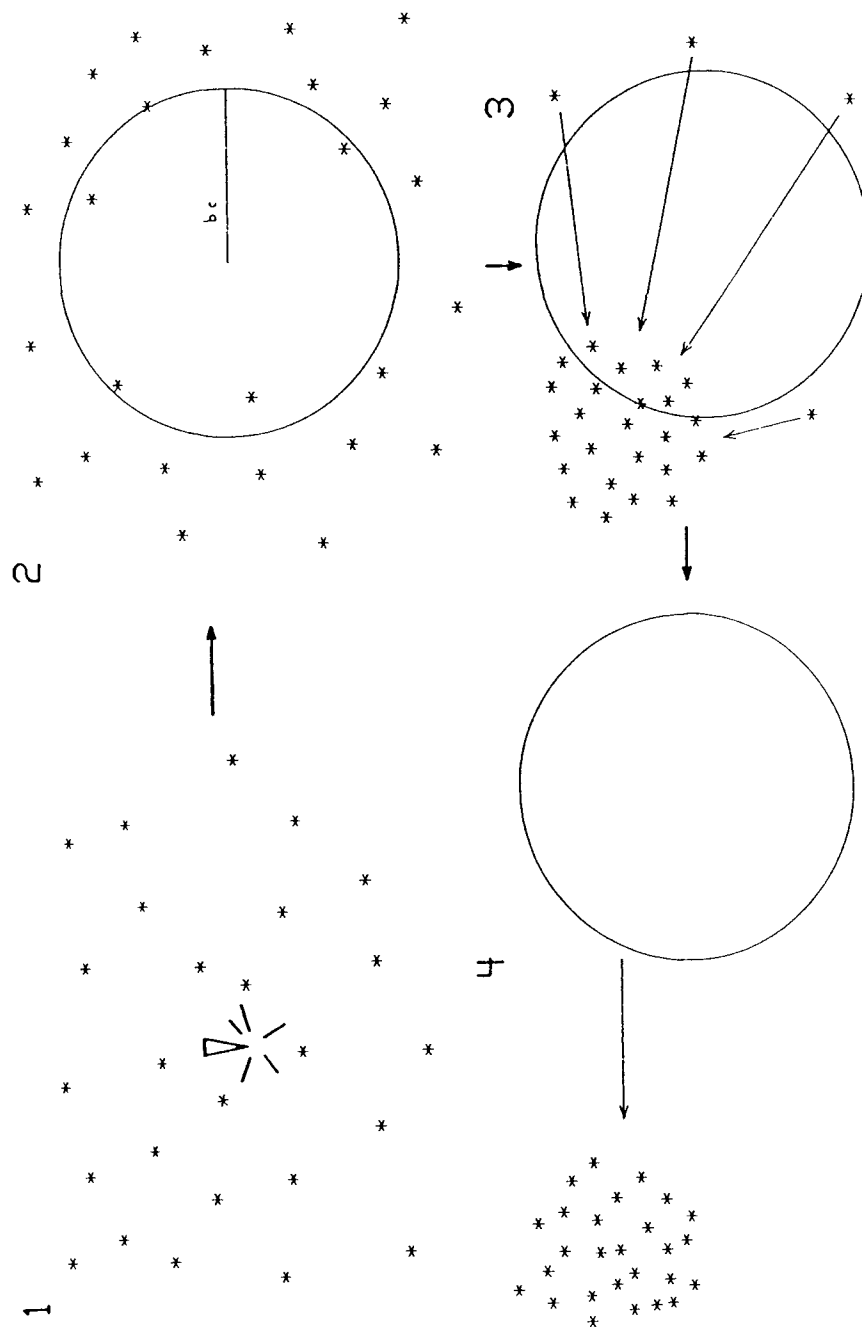Figure 15. Surfperch flight response, individuals.

Figure 16. Surfperch response to disturbance.

secs.) into a much tighter group. Note that one effect of this schooling behavior, as qualitatively shown in Figure 16, is that the school has become a single and perhaps more easily seen mass. The ramifications of this phenomenon will be discussed later.

The reactions of the surfperch as a school were again tested after the fish had formed the more cohesive school described above, i.e. after at least one initial disturbance had been performed. The flight distances of the school as they exhibited a type 1 evasive burst were measured from the center of the school at its initial position to its center at its final position. Figure 17 plots the flight responses of the school again as function of the school's distance from the point of disturbance. The relationship here is described by the equation FD = -.31DD + 1.171, (n = 23, standard error of y estimate .39, r^2 = .62, x coefficient p <.001). The threshold of reaction of the school to a strike disturbance is 3.8 meters, identical to that of the individuals fish.

The Flight Responses of Staghorn Sculpins
Leptocottus armatus

The flight behaviors of Staghorn Sculpins (henceforth referred to as sculpins) were much more complex than the simple schooling response of surfperch, and are thus
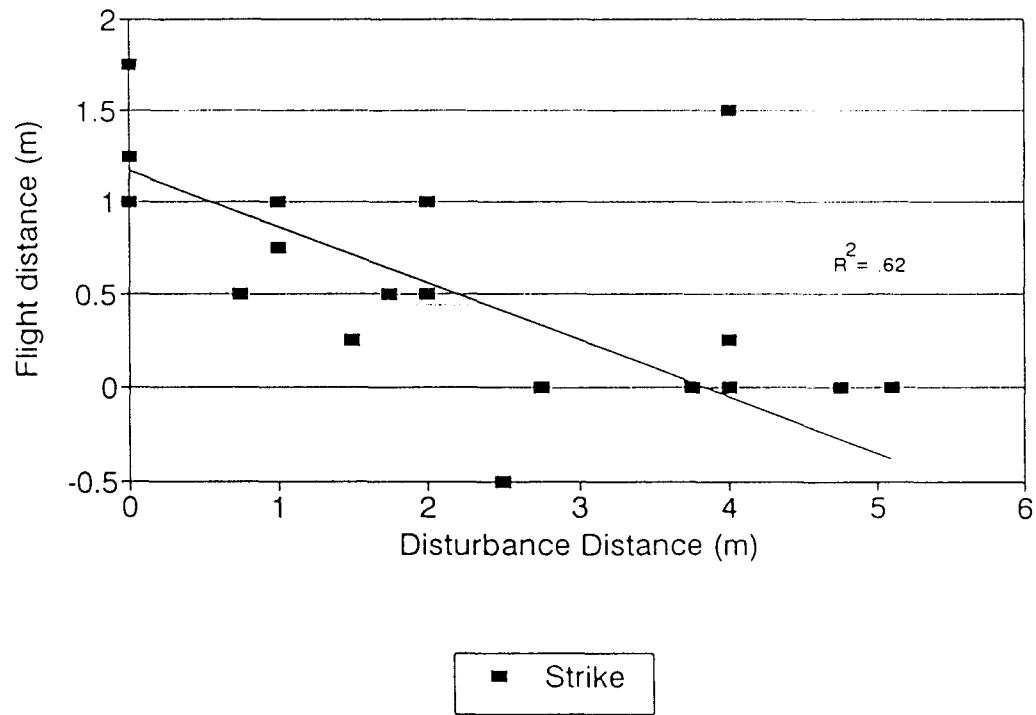
Figure 17. Surfperch flight response, school.

described in considerably more detail. In addition to the simple evasive distances travelled, other factors that might have influenced sculpin response - individual orientation to the strike, degree of sedentarity and crypsis (dug in, not dug in) and size class - were recorded and analyzed. As sculpin flight responses were clearly defined by abrupt stopping points, no analysis of their swimming speeds was necessary to describe those responses. Sculpin swimming speed was 2.5-3.0 m/sec.

Sculpin flight distances are plotted against the disturbance distances in Figure 18. In 37 of 209 trials (18%) sculpins reacted to the withdrawal of the head, presumably having seen it. As this experiment was intended to primarily be a test of responses to the concussion of a striking heron, only those behaviors occurring in response to the head impact (after the drop and before withdrawal) were included in the analysis. Though a t-test of the x coefficient reveals the significance of the correlation between disturbance distance and flight distance (n = 209, std. error y est. = .979, t = -3.838, P <.001) the very low r^2 value (.07) indicates that disturbance distance is a very poor predictor of flight response, accounting for only 7% of the variance in that behavior.

A striking feature of the response of sculpins was the predominance of the "zero response," where no flight behavior or reactive movement of any kind was noted. On the
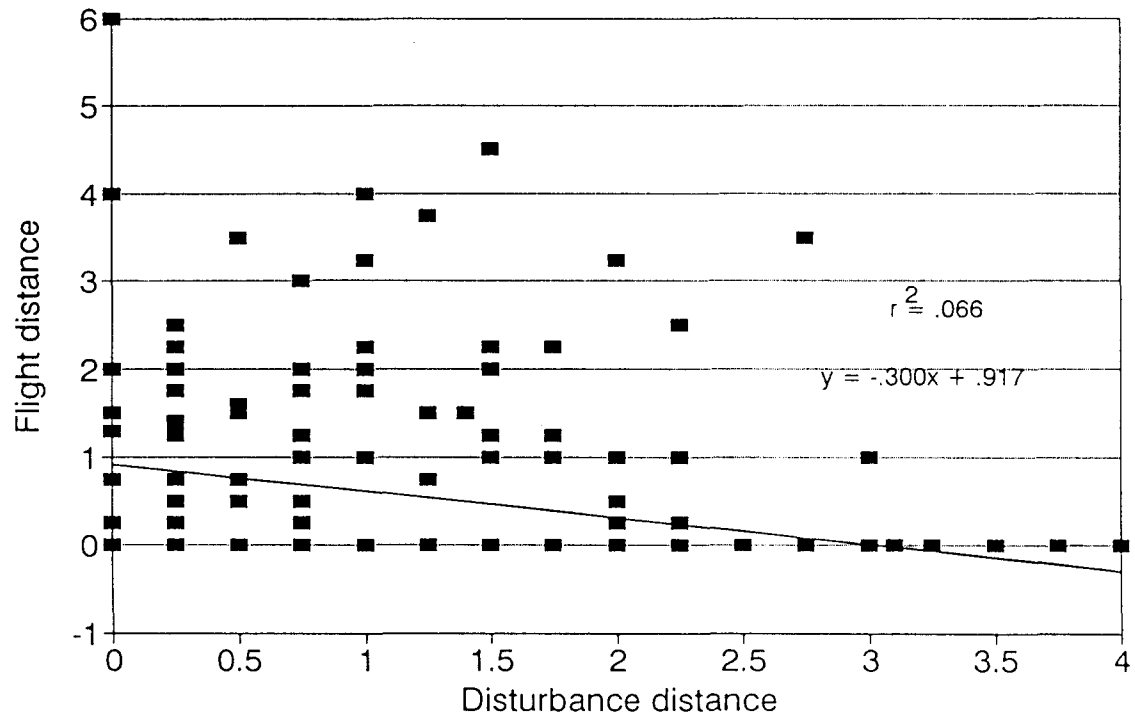
Figure 18. Sculpin flight response, strike, response = zero cases
included.

possibility that the zero response (flight distance = 0) was responsible for the correlation between disturbance distance and flight response, the percentage of sculpins responding to the strike disturbance was analyzed with respect to the disturbance distance (Figure 19). A R x C test of independence rejected the null hypothesis that the percentage of fish reacting to the strike was independent of disturbance distance (G = 43.58, P << .001). To confirm the zero response effect on the correlation of flight distance and disturbance distance, those cases were eliminated and flight distance was replotted against disturbance distance (Figure 20). Regression analysis now showed no significant correlation (FD = .029DD + 1.643, n = 63, T = -.351, P > .73, squared multiple r = .002) between flight distance and disturbance distance.

Given the possible importance of the zero response exhibited by sculpins in terms of the foraging strategies of wading birds, further analysis of this behavior was warranted. One behavior recorded for sculpins that seemed correlated to the zero response was the "dug-in" behavior. Here, the sculpin would partially bury itself in the substrate, using its large pectoral fins to displace and redistribute sediment on and around its body. The degree to which a fish could bury itself in the experimental conditions was restricted by the size of the animal; large class fish could bury only their pectoral fins and the
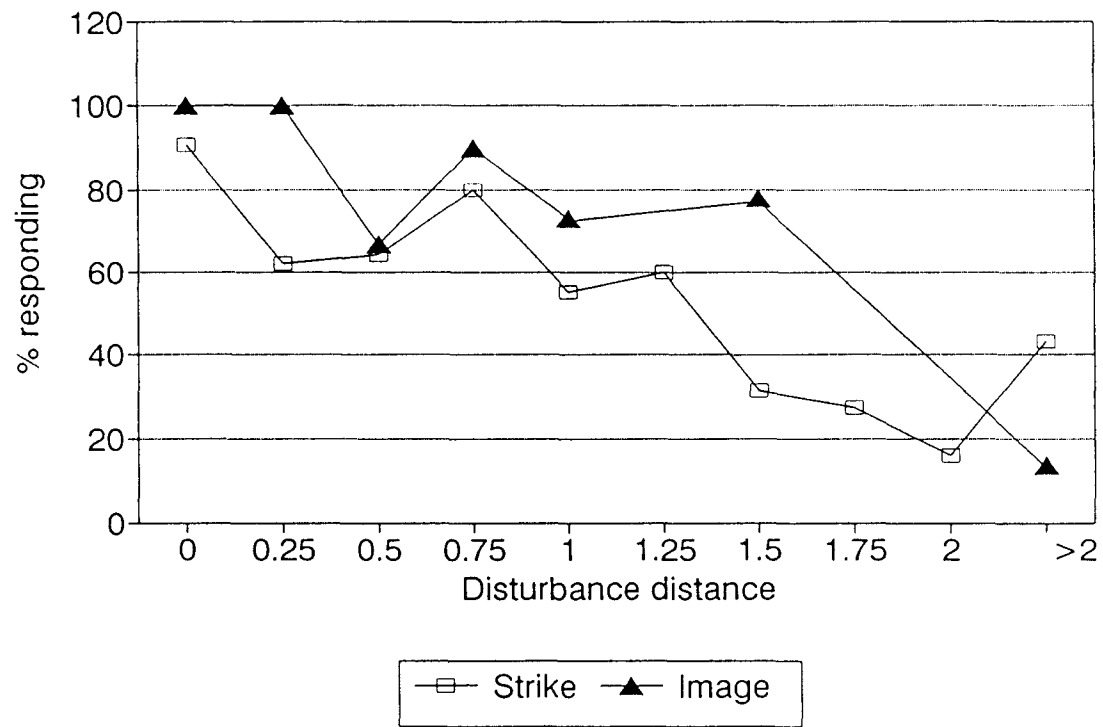
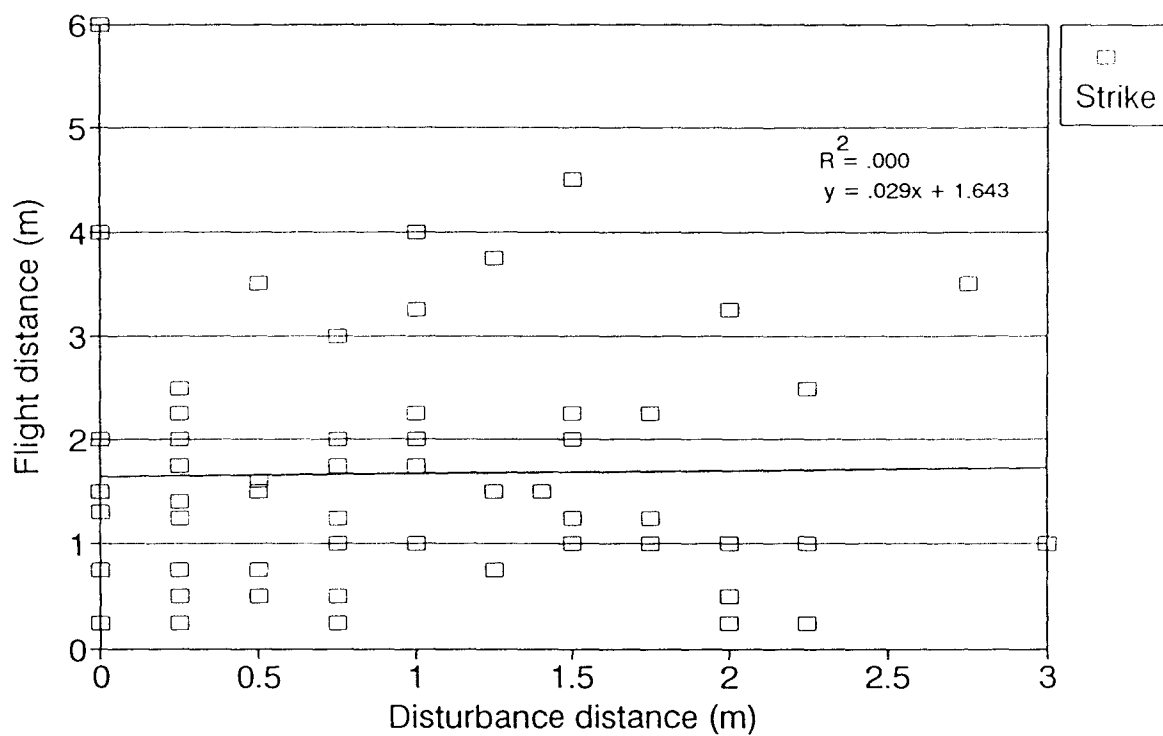Figure 19. Percentage of sculpins responding to strike and image disturbances.

Figure 20. Sculpin flight response, strike, response = zero cases excluded.

ventral quarter of their bodies, whereas the small size
class fish could bury themselves until only the very dorsal
anterior portions of the head and eyes protruded. The
percentage of dug-in fish responding to the strike
disturbance vs the percentage of not dug-in responding is
shown in Figure 21. Contingency table analysis showed
significant differences (P < .001) in the percentage of fish
responding at 0.0, 0.25, 0.5, and 1.5 m disturbance
distances, as well as 0.75 and 1.0 m (P < .05).

Given then the fact that sculpins are more likely to
react to a disturbance if not dug-in, the zero
response/disturbance distance relationship was re-examined.
As was shown in Figure 19, the percentage of fish responding
declined with the increasing disturbance distance. Plotting
the percentage of those dug-in at the respective disturbance
distances (Figure 22), however, shows that the strong
correlation seen between zero response and disturbance
distance was in part an artifact of the increasing
percentage of observed fish dug-in at those distances. This
is not to say that there is no relationship between the
percent responding and the disturbance distance; the data
represented by Figure 21 clearly show a decline in the
number of not dug-in fish responding as disturbance distance
increases. For dug-in fish, however, this relationship is
less clear.

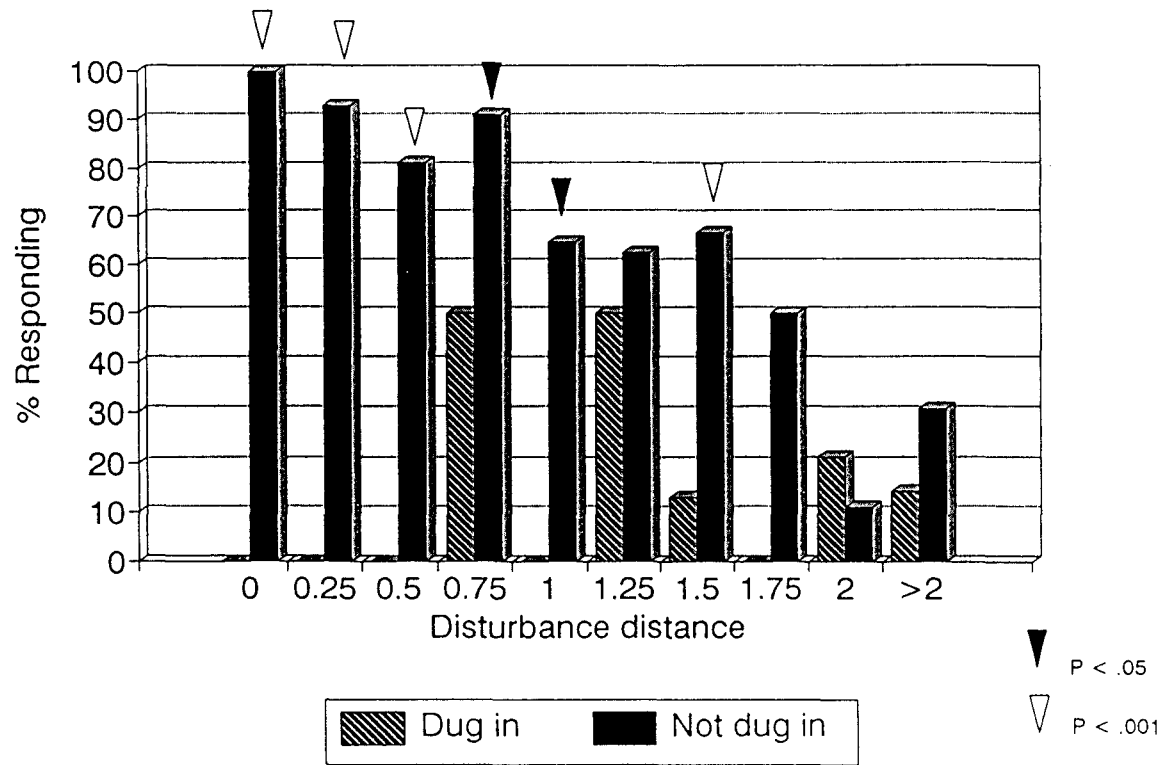As previously stated, the high number of zero response

Figure 21. Percentage of sculpins responding to a strike disturbance, dug in and not dug in.
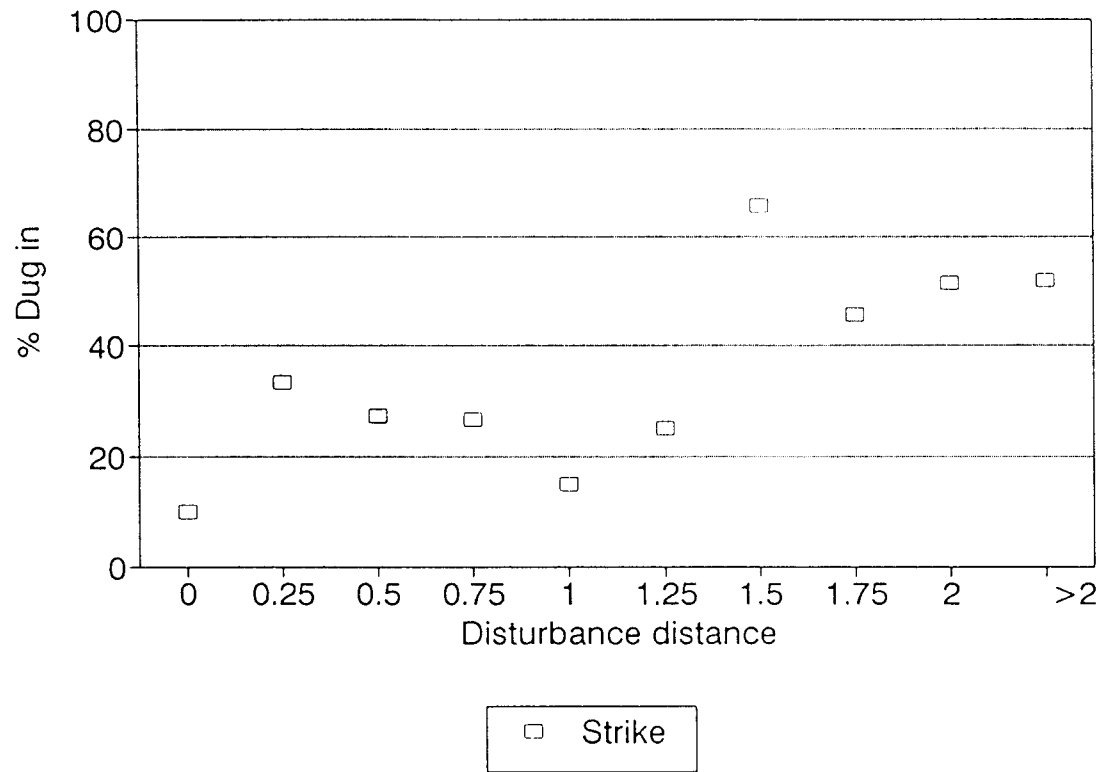
Figure 22. Percentage of sculpins dug in at respective disturbance
distances, strike.

cases of sculpins to the heron head strikes raised the
question of whether the simulated strike was an appropriate
stimulus to use in the study of sculpin flight responses.
Thus, experiments were conducted using the image of a Great
Blue Heron, which was lowered into the tank to present a
visual disturbance. As this was a test of a visual
stimulus, all responses to the image, including those
occurring as the image was lowered or withdrawn were
included in the analysis. The resulting flight responses
are shown in Figure 23. Initial regression analysis yields
$FD = -.93DD + 3.68$, with $n = 87$, x coefficient $t = -5.46$, $P
< .001$, and $r^2 = .26$. As with the strike disturbance data,
the relationship between the percentage of "zero response"
cases and disturbance distance (Figure 19) was analyzed by a
R x C test for independence and found to be highly
significant ($G = 48.21$, $P << .001$). These data are not
compromised by an increasing percentage of dug in fish at
the greater disturbance distances (Figure 24) as was the
case for the strike data. The zero response cases were
eliminated and flight response was again regressed against
disturbance distance (Figure 25, $FD = -.62DD + 3.97$, with $n
= 58$, x coefficient $t = -1.53$, $P > .13$, $r^2 = .04$) showing
that the zero response cases were primarily responsible for
the significant linear relationship of flight distance and
disturbance distance. A contingency table analysis of the
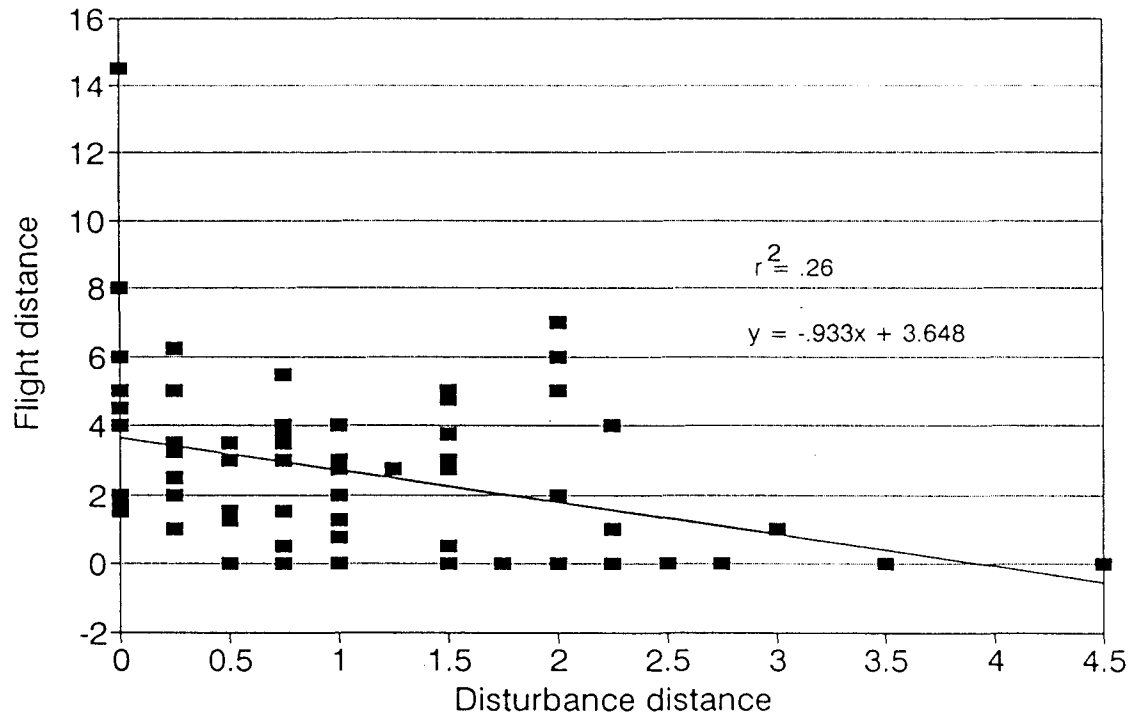disparate responses of "dug in" and "not dug in" fish showed

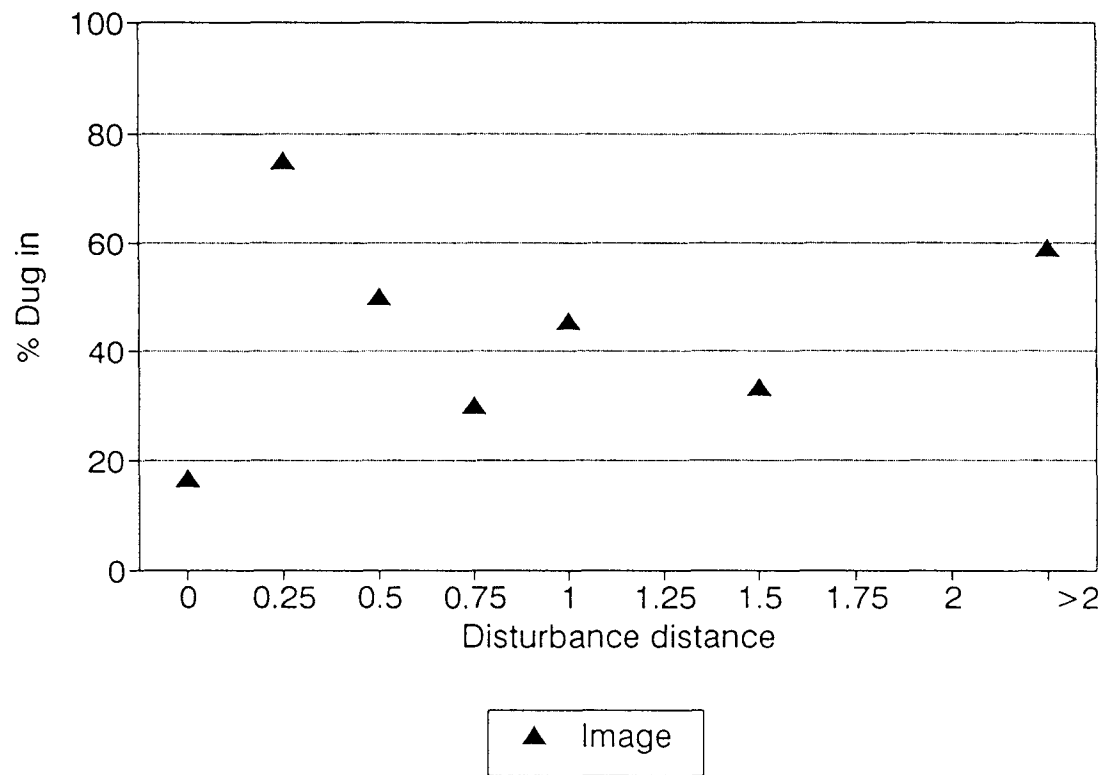Figure 23. Sculpin flight response, image, response = zero cases included.

Figure 24. Percentage of sculpins dug in at respective disturbance
distances, image.
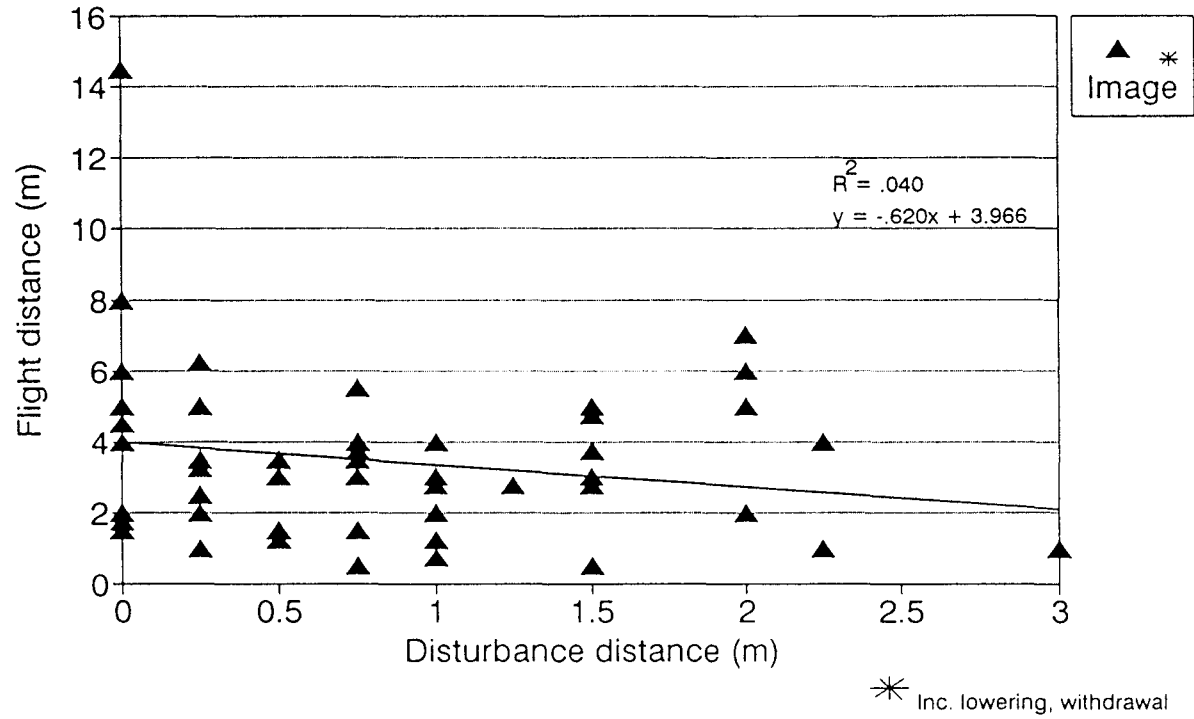
Figure 25. Sculpin flight response, image, response = zero cases excluded.

significant differences in zero responses for disturbance distances of 1.0 and 1.5 meters ($P < .05$, Figure 26). These data also show the increasing zero response with increasing disturbance distance.

Sculpin flight responses by size class are shown in Figures 27, 28, and 29, and regression analyses results are shown in Tables 3 and 4. For the strike disturbance with zero response cases included, significant relationships between flight and disturbance distance were found in size classes 1 and 2 ($P = .001$ and $.007$ respectively); though with zero response cases excluded, regressions again revealed no significant correlations ($P = .610$ and $.280$ respectively). For image disturbances with zero response cases included, significant correlations were found in size classes 1 ($P = .007$) and 2 ($P = .006$), though the correlation in class 1 disappears when zero response cases are excluded ($P = .800$).

As disturbance distance had little influence on flight distance (disregarding zero responses), the flight distances of each class were combined and regressed with size class (Figure 30). There was no significant difference in the flight distances of the three age classes ($P > .10$ for image, $P > .13$ for strike disturbance). The mean flight distance for all sculpins when excluding zero response cases was 1.64 m ($n = 63$, sd = 1.17) for the strike disturbance; mean flight distance for the image disturbance was
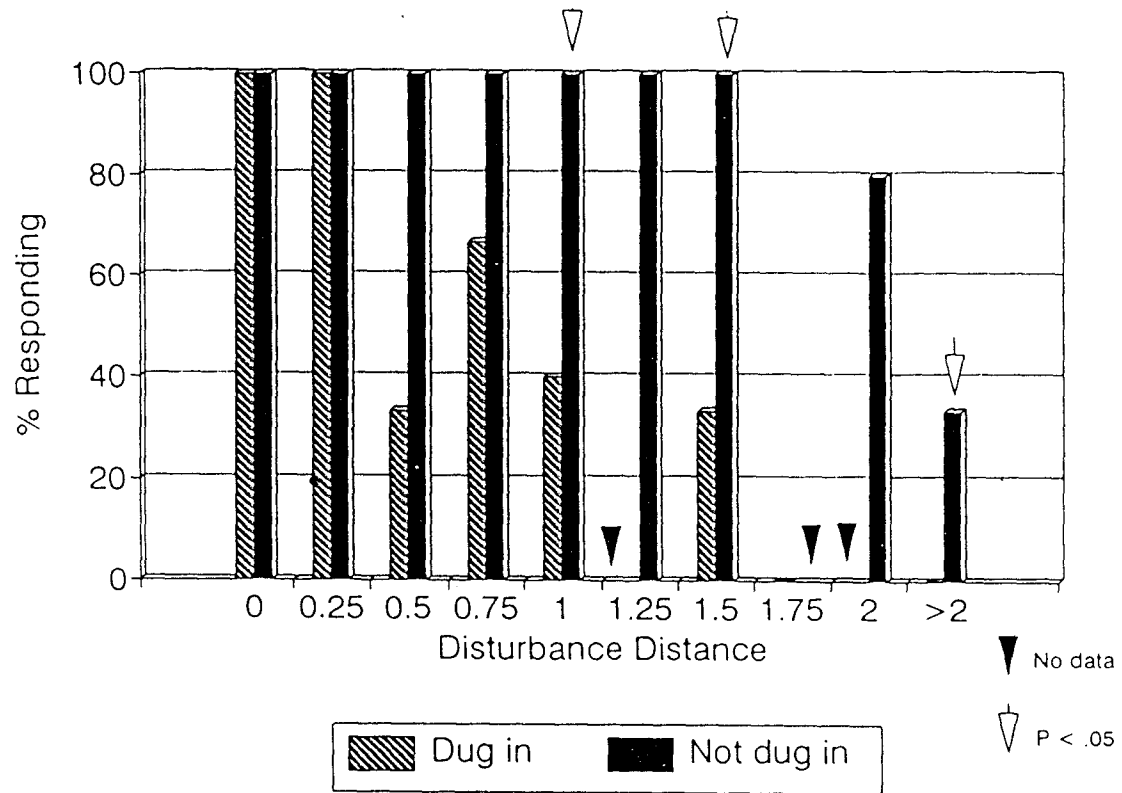
Figure 26. Percentage of sculpins responding to image, dug in and not dug in.
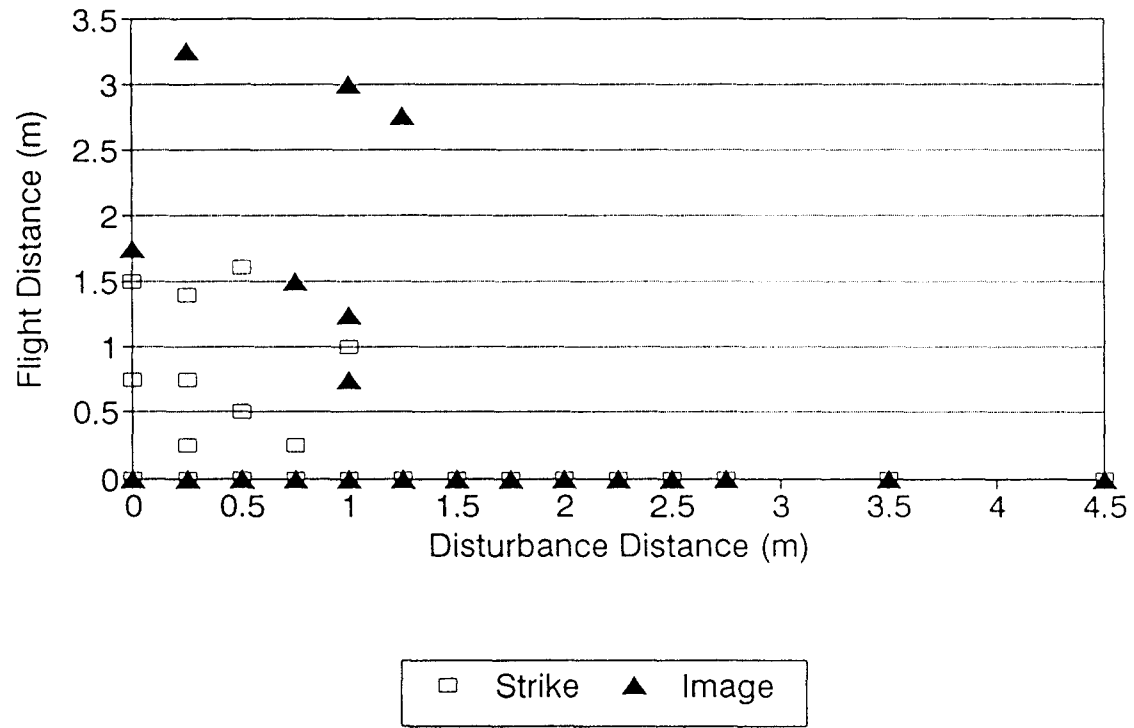
Figure 27.   Sculpin flight response, size class 1.
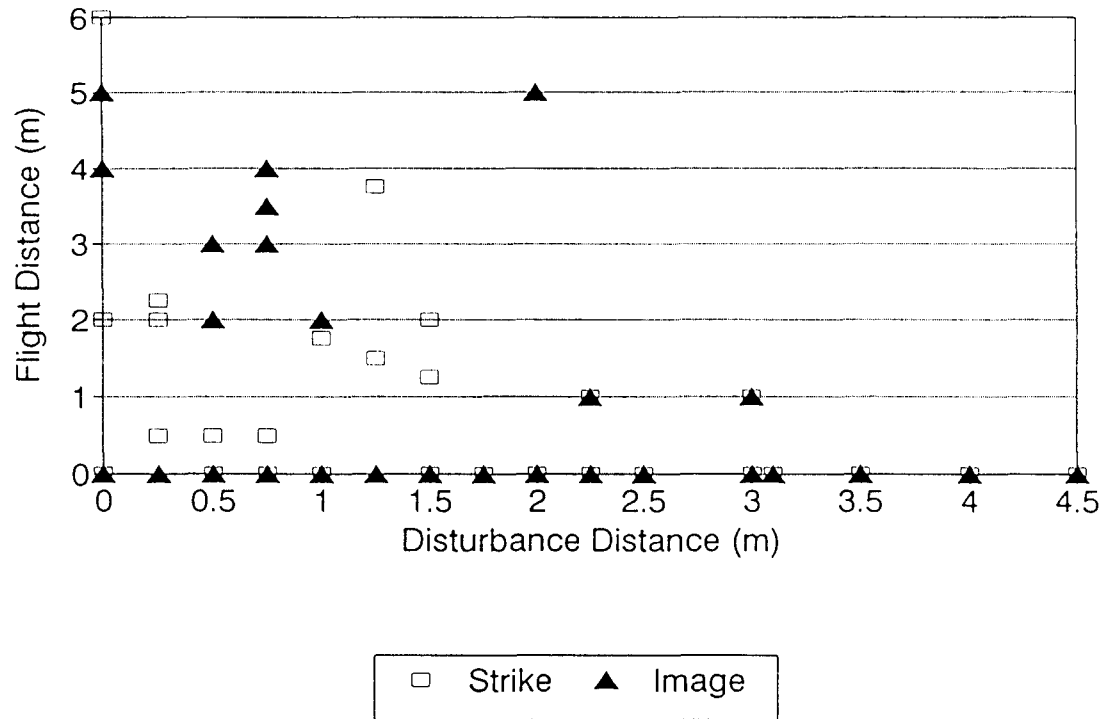
Figure 28. Sculpin flight response, size class 2.
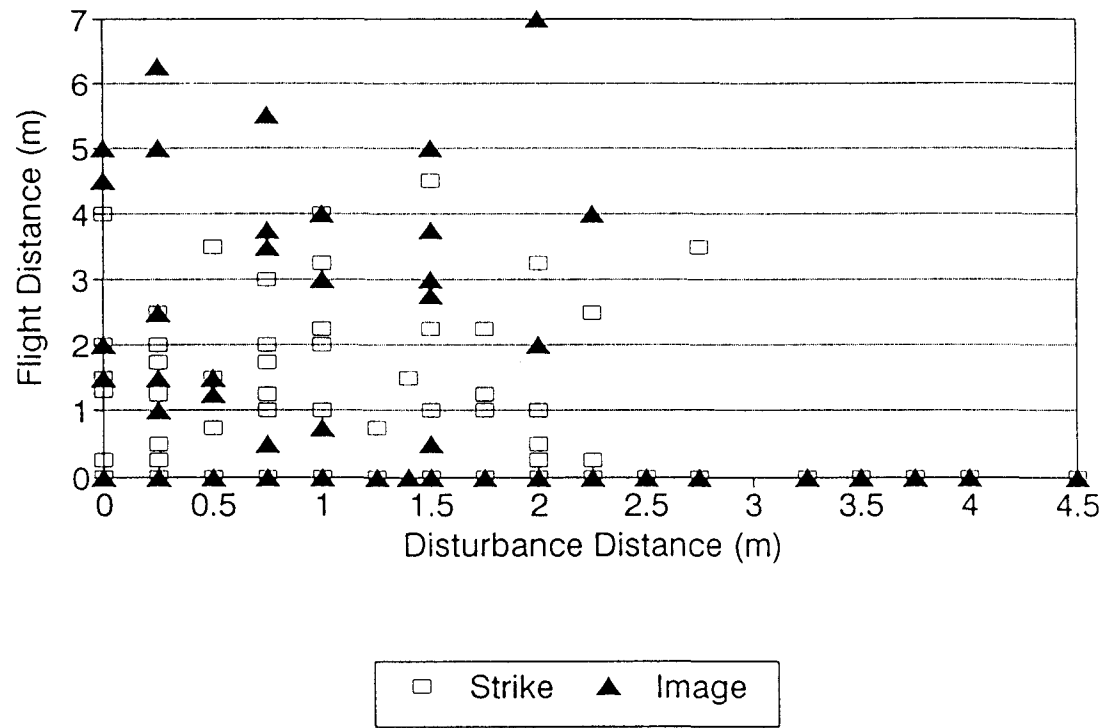
Figure 29. Sculpin flight response, size class 3.

Table 3. Regression Analyses for L. armatus Flight Response
          Distance as a Function of Disturbance
                Distance, by Size Class,
                Disturbance = Strike

Size class	Inc. 0 = response?	n	Regression equation	r^2 adjusted	t of x coeff	P
1 (<8.5 cm)	yes	45	FD=−.27DD+.51	.22	−3.70	.001
	no	9	FD=−.30DD+1.01	.00	−.53	.610
2 (8.6 − 10.1 cm)	yes	53	FD=−.48DD+1.20	.12	−2.81	.007
	no	14	FD=−.52DD+2.37	.02	−1.13	.280
3 (11.0 − 14.0 cm)	yes	42	FD=.56DD+.74	.00	.96	.345
	no	24	FD=.62DD+1.454	.00	.96	.347

FD = Flight Distance; DD = Disturbance Distance

Table 4.   Regression Analyses for <u>L. armatus</u> Flight Response
          Distance as Function of Disturbance
                Distance, by Size Class,
                   Disturbance = Image

Size class	Inc. 0 = response?	n	Regression equation	r^2 adjusted	t of x coeff	P
1 (<8.5 cm)	yes	17	FD= -.44DD+1.79	.36	-.313	.007
	no	7	FD= -.25DD+2.22	.00	-.267	.800
2 (8.6 - (10.1)	yes	22	FD= -.90DD+3.13	.28	-3.055	.006
	no	13	FD= -.90DD+4.04	.29	-2.429	.033
3 (11 .0 - 14.0 cm)	yes	25	FD=-1.21DD+3.36	.00	-1.014	.321
	no	24	FD= -.99DD+3.55	.00	-.904	.376

FD = Flight Distance;   DD = Disturbance Distance
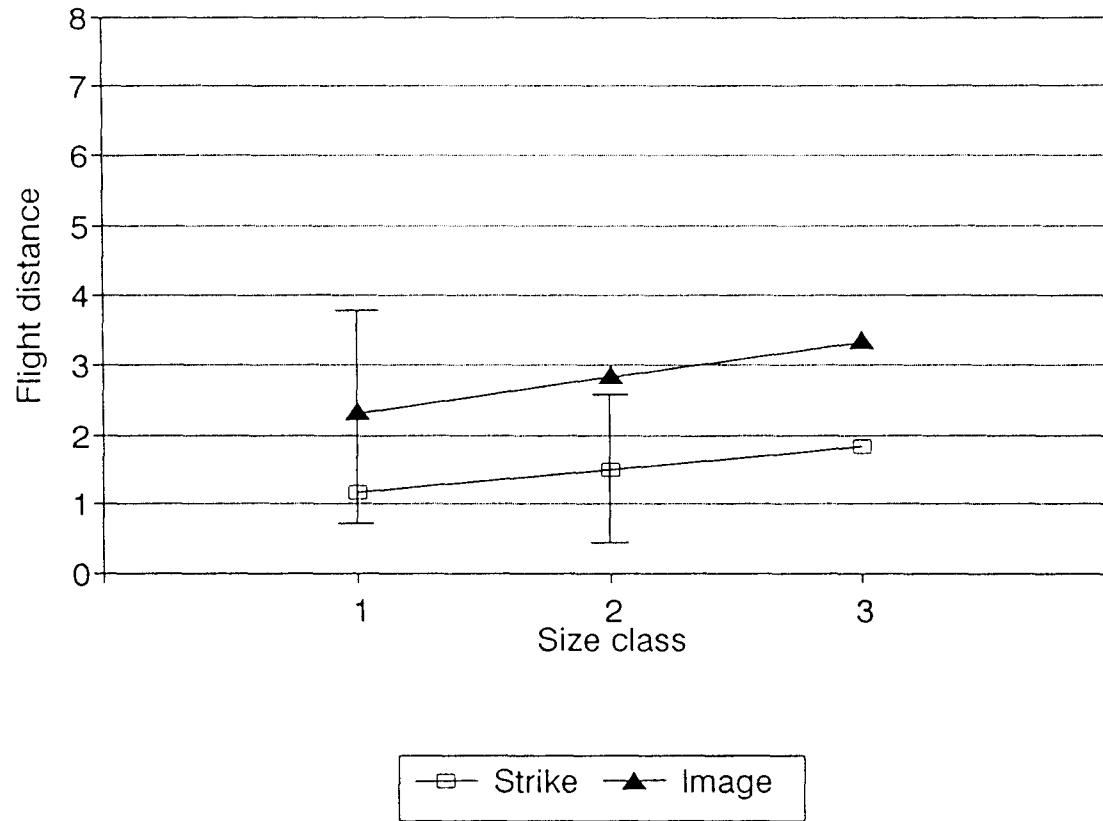
Figure 30. Sculpin flight response by size class.

significantly higher (P < .001) at 3.474 m (n = 58, sd = 2.27).

Though not subjected to a statistical test, the size classes seemed to show a disparity in disturbance distance threshold (size class 1, 1.25 m; 2, 3 m; 3, 2.75 m).

Fish in a given area may all orient in the same direction due to current or other environmental factors; as this orientation could conceivably be a factor influencing their response to a heron, the orientation of the fish to the disturbance was recorded. The orientation of the fish was transformed from 0 - 180 degrees to a coefficient of 0 - 1, 1 being facing directly toward, .5 being 90 degrees to the point of disturbance, 0 facing directly away. With the zero response cases excluded, a multiple regression analysis was used to examine the influence of sculpin orientation (Figures 31 and 32). No significant effect of orientation was seen in either the strike or the image (Strike : Disturbance distance t = -.81, P = .42, orientation t = 1.29, P = .20; ANOVA F-ratio 1.05, P = .36). Image: Disturbance distance t = -1.47, P = .15, orientation t = 1.88, P = .07; ANOVA F-ratio 2.98, P = .06), though the combined effects of orientation of fish and disturbance distance in image disturbances may warrant further investigation. A lack of influence of the sculpin's orientation to a disturbance is not surprising; as their eyes are dorsally located on the head and somewhat
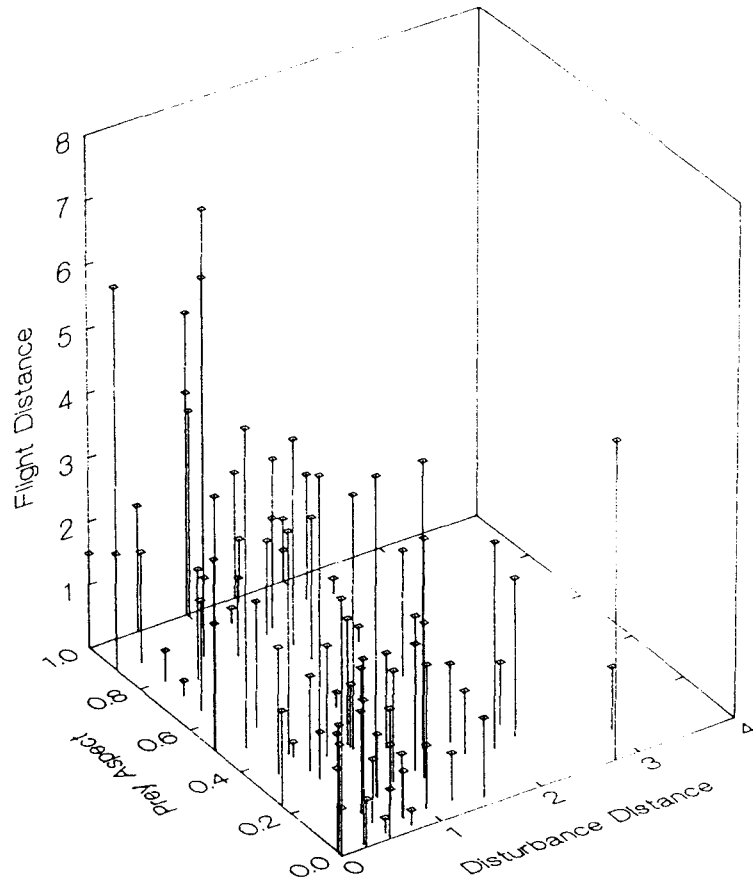
Figure 31. Sculpin flight response, prey aspect, strike disturbance.
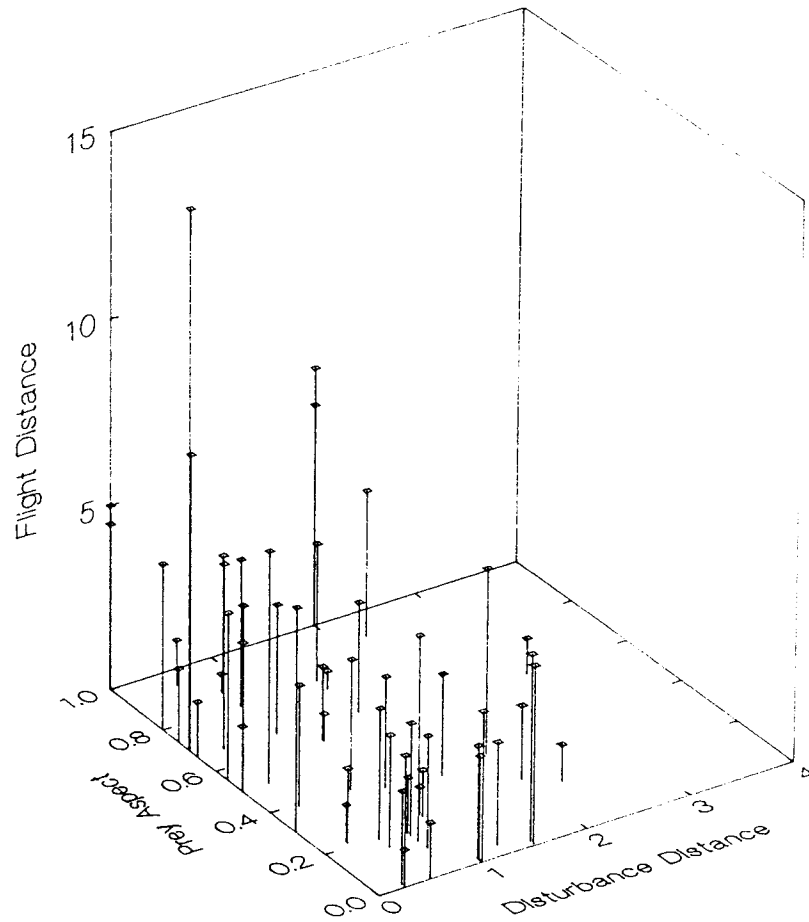
Figure 32. Sculpin flight response, prey aspect, image disturbance.

protruding, they could easily scan a 270° field of view. The data showing greater response distance of sculpins to the image and the greater influence of orientation on the flight response indicate that the Staghorn sculpin may to a considerable degree rely on visual cues to avoid predation.

The final analysis of sculpin behavior conducted was a measure of their level of activity before and after the disturbance experiment sessions. Sculpin movements greater than 25 cm were counted for 10 minutes prior to and 10 minutes immediately following the disturbance experiments (Figure 33). A t-test shows that the mean number of sculpin movements before being disturbed (mean = 59.1, sd = 30.7) is significantly higher than the number following (mean 7.1, sd = 6.7, P < .002).

Discussion

Flight Responses of Shiner Surfperch

The purpose of this study was to describe the flight behaviors of two principal Great Blue Heron prey species that those behaviors could be incorporated into the geometric model described in Chapter II. Shiner Surfperch behavior approximates the behavior described by the "bomb crater" geometric model; that is, the flight distance of the individuals increases with their proximity to the

Figure 33.   Sculpin movements, greater than 25 cm, before, after
disturbances.

disturbance, and all individuals closer than the disturbance
threshold will react to the disturbance. The result is the
ephemeral circle *bc* illustrated in Figure 1, after which the
school reforms and moves away (Figure 16). Once reformed in
a more compact school they have become, in smaller scale,
the patchy resource thought to select for social foraging.
With the prey now occupying less space, the chance of a
single foraging heron happening upon them has diminished;
with numerous herons foraging in the same area, there would
be a greater chance of an individual heron finding the
school again, allowing the other individuals to cue on the
bird's behavior.

It is evident, however, from this study's foraging data
on egrets and herons that being a solitary forager does not
preclude capture of surfperch. Surfperch associate very
strongly with the eelgrass <u>Zostera</u> <u>marina</u>, (Bayer 1981), and
personal observations of surfperch around docks and in the
disturbance experiments, where they rarely strayed from the
walls of the tank, suggest they may at times be extremely
predictable in terms of their distributions. Moreover,
their adherence to refugia may also make their flight
behaviors predictable. On several occasions, Great Egrets,
Great Blue Herons and Green-backed Herons (<u>Butyroides</u>
<u>striatus</u>) were seen repeatedly taking surfperch (maximum of
7 in a 10 minute period by a Green-backed Heron) from the
boat launch dock in Haynes Inlet. Similarly, the study fish

would rarely leave the walls of the tank, even though the majority of disturbances occurred on the tank's perimeter. The fact that the school remained on the perimeter may have been by default, however, as the fish merely attempt to exhibit their normal ranging within the confines of the tank. To examine the possible refuge effect and distinguish it from this edge effect, a preliminary study of surfperch in the presence of a refuge other than the walls of the tank was conducted during their final two days of captivity. A 1m x4m artificial eelgrass bed constructed of green plastic strips (cheerleader's "pom-pom" material) glued to aluminum mesh and placed in the center of the experimental tank (beneath disturbance points 12 and 13, Figure 13) to provide a realistic refuge. After 24 hours, with the fish having dispersed into their characteristic loose school, a strike disturbance was performed. After dispersing and reforming into the cohesive defensive school, they moved 3 m into the eelgrass bed and remained there for 4 minutes. Another strike disturbance was then created (#13), disturbing the school to the far left end of the eelgrass. Within 1 minute, however, the entire school had returned, without prompting, to directly under the #13 disturbance point. The school was disturbed 3 minutes later, again by striking head #13; they dispersed briefly, but had reformed in the eelgrass less than 1 minute later, now directly under disturbance point #12. Disturbed then by #12, the school

dispersed, reformed under #13 12 seconds later, and within 45 seconds, had returned to directly under #12. The experiment was repeated the following day, with nearly identical results - after fleeing to the artificial eelgrass bed, the school would endure multiple disturbances in close proximity rather than leave the refuge of the eelgrass bed. The possible reasons for the surfperch's entrainment in the eelgrass are worthy of mention. First, the allure of the refuge may simply be too great to ignore; i.e., the benefits of such a refuge in decreased exposure to other predators outweighs the exposure to predators cuing on the refuge - the "better the devil you know" hypothesis. Alternatively, the school may simply be demonstrating a lack of spatial awareness as to the location of the last disturbance. In this case, though the flight response of the individuals close to the disturbance is initially straight away from the disturbance, they soon encounter individuals more distant from the point of disturbance that are not reacting as strongly. At this point, the schooling behavior begins to dominate, and the spatial awareness of the individuals with good information about the location of the disturbance is eroded by the movements of the school.

Before labelling this behavior as maladaptive, one must consider the life history of Shiner Surfperch. In the winter months, this species resides offshore at depths from 18 to 128 meters (Emmett et al. 1991). In the spring, they

move into bays and estuaries to bear live young. During

this period they are strongly associated with eelgrass,

particularly at night (Bayer 1981). Within these dissimilar

habitats reside a wide range of predators, from large marine

fishes such as sturgeon (Acipenser spp.), salmon

(Oncorhynchus spp.), rockfish (Sebastes spp.), and lingcod

(Ophidon elongatus) (Emmett et al. 1991) to marine mammals

such as Harbor Seals (Phoca vitulina) (Simenstad et al.

1979, pers. obs.) and such birds as cormorants

(Phalacrocorax spp.), Bald Eagles (Haliaeetus lecocephalus),

Osprey (Pandion haliaetus), Caspian Terns (Sterna caspia),

Kingfishers (Megaceryle alcyon), Great Blue herons and

egrets, (Emmett et al 1991, pers obs.). For a fish of

generalist morphology and habitats encountering a host of

predators whose tactics range from ambush from within the

water (lingcod, rockfish) to pursuit through the water

(salmon, Harbor Seals, cormorants) to ambush from above the

surface (terns, herons), schooling may be an effective all-

around anti-predator behavior (Pitcher 1986). It may not,

however, be effective in its ability to react spatially to

the presence of predators when the disturbance created by

the predator is a single brief event, or multiple but

distinct events. The length of the interaction of surfperch

with predators actively pursuing them within the water is

temporally protracted when compared with the point

disturbance created by a plunging heron, and may serve to

provide a greater stimulus by which the school can correctly

gain a spatial awareness of the location of that predator.

Conversely, the extremely compact and disjointed stimuli of

a striking heron may not provide the school with information

sufficient to effect the movements of the entire school, and

the information is eroded and lost to the instinct to

school. This effect may be important to foraging wading

birds, particularly to Great Blue Herons, whose summer diet

and nesting success may depend on efficient foraging on

surfperch. It may also allow socially foraging herons to

drive fish and thereby forage more efficiently. In any

case, a study of spatial learning in surfperch with regard

to disturbances created by wading bird predators would be

extremely interesting, particularly if contrasted with the

abilities displayed by the other subject discussed here, the

Staghorn Sculpin.

Flight Responses of the Staghorn Sculpin

To assess the possible influence of sculpin flight

response on wading bird foraging strategy, the following

aspects of sculpin behavior described in this study are

discussed within the context of the geometric model.

1) Flight distance. Sculpins did not conform to the "bomb

crater" geometric model, i.e. the lack of negative

correlation between flight distance and disturbance distance

would not result in the concentration of individuals on the perimeter of a circle *bc*. Without this predictable response a solitary heron would gain nothing from foraging using the square search tactic (Figure 9), nor would adjacent socially foraging herons benefit in the disturbance facilitated foraging manner depicted in Figures 10 and 11. Furthermore, with a threshold for any reaction at < 3 m, herons would need to be foraging in extremely close quarters, in which case substrate disturbance that would further mask sculpins might begin to influence foraging efficiency.

2) The zero response case. This is perhaps the single greatest behavior that would contribute to the inability of wading birds to herd prey or otherwise benefit from social foraging. Data show that if sculpins are engaged in maximum crypsis i.e. dug in, they are extremely unwilling to abandon that defensive tactic, even when presented with the image of a heron 0.5 to 1.0 m away (Figure 25). In the case of a concussive disturbance only, at no disturbance distance did the number of dug in sculpins reacting exceed 50% (Figure 20). The behavior to remain cryptic when confronted with only a lateral line stimulus is easy to understand; presumably only a small percentage of such stimuli are potential threats, and it would defeat the purpose of a cryptic morphology to react to all the "noise" in the environment. To remain cryptic when presented with a visual stimulus (Figure 25), however, could be considered a more

deliberate behavior to avoid predation, and one that would not lend itself to any social foraging tactics employed by wading birds.

3) The cessation of routine movements after being disturbed. As stated, the degree to which a sculpin may be employing crypsis as a defensive tactic determines whether or not it reacts to a disturbance, which in turn may determine the success of social wading birds attempting to drive or herd fish. The data on routine (non-disturbance related) movements (Figure 33) indicate that wading bird type disturbances result in a decrease in sculpin movements - and the concomitant increase in crypsis. The data were insufficient to test if this decrease in general activity was accompanied by an increase in zero response cases (a multiple regression of percent responding against the independent variables of disturbance distance and number of previous disturbances in the session). The simple decrease in routine movements itself, however, would result in an increase in search time for herons. With multiple herons in an area, the ability to simply walk a short distance away from a site just disturbed to an undisturbed site where sculpins may still be engaged in routine movements is lost to the individual heron.

No data on the spatial awareness and learning was gathered for sculpins. Bayer (1981) did show, however, that Staghorn Sculpins were more abundant in open mudflats than

the eelgrass entrained Shiner Surfperch. This would indicate that sculpins, by virtue of superior crypsis, might be less inclined to have their flight behaviors dictated by the presence of an eelgrass bed or any other refuge, and their flight responses would consequently be less predictable. More seriously, in terms of heron efficiency, the presence of numerous herons in an area may, regardless of that area's refuge quality, quickly result in sculpins leaving that area - possibly into unforagably deep water.

Meyerriecks (1960) and Heathwole (1965) showed evidence for increased efficiency for social Cattle Egrets (Bubulcus ibis) as they forage for insects in dense grasslands. Goss-Custard (1977) showed, however, that increases in flock size increased density dependant agonistic behaviors and resulted in decreased foraging efficiency in wading birds. Goss-Custard also showed (1970) that in Redshanks (Tringa totanus, order Charadriiformes, family Scolopacidae) prey availability and foraging efficiency decreased due to disturbance by proximal conspecifics when feeding on relatively sedentary crustaceans. The data from this study indicate that due to the flight responses of Staghorn Sculpins, herons could gain nothing, and perhaps decrease their efficiency, by foraging socially for these prey.

In considering these flight responses that differ dramatically from those of Shiner Surfperch, it is useful to examine other aspects of the Staghorn Sculpin's life history

and the other selective pressures it encounters. Though older and larger sculpins may move to deeper offshore waters, this is primarily an estuarine species, with most individuals spending their entire lives in estuaries (Emmett et al. 1991). Bayer (1981) found that Staghorn Sculpins were the only species consistently found in appreciable numbers throughout the year in both eelgrass and upper intertidal mudflats; in the latter habitat, they constituted 54% of the biomass of fish. As such, Staghorn Sculpins are probably a staple part of the diet for the resident populations of herons throughout the year. It is also known to be preyed upon by Harbor seals, loons (Gavia spp.) cormorants and gulls (Laurus spp.), as well as large fish (Emmett et al. 1991, pers. obs.). The Staghorn Sculpin does not school as a defensive tactic (pers. obs.) instead depending on crypsis facilitated by its ability to partially bury into the soft substrate. If captured, the Staghorn Sculpins will erect pre-opercular spines armed with needle-sharp recurved hooks (hence "staghorn") to hinder predator swallowing. This armament can be extremely effective; on 5 occasions (4 juveniles, 1 adult) herons were seen gagging and expelling sculpins from their throats, with no attempt to retrieve them after they had been dropped. Adult Great Blue Herons nearly always handle captured sculpins extensively, particularly about the head and by the spines, sometimes even carrying larger sculpins to shore and

repeatedly spearing them in an effort to lower the spines. This behavior may indicate that some learning is involved in correctly handling sculpins. The consequences of attempting to swallow too soon without proper handling can be more grave than simply losing a meal; a Great Blue Heron found dead and examined at the Institute of Marine Biology was found to have died as a result of a large sculpin lodged in its esophagus. As it may be germane to the analysis of herons foraging rates for this species, it should be noted that the costs of handling sculpins may at times be too great if other more efficiently taken prey are available. On one occasion, a Great Blue Heron foraging at Sitka Dock area after having taken several of the unidentified cod species, (which were handled on average in less than 21 seconds, sd = 12 seconds) captured a 12 cm sculpin, carried it to shore, set it down on a mat of eelgrass at water's edge, and walked away to continue foraging. Handling time data gathered indicate the heron would have spent an average of 1.5 minutes, and up to 3 minutes handling a sculpin of equal size. Given the physically hearty nature of this species (Emmett et al. 1991, pers obs.) it is likely sculpins survive such encounters.

CHAPTER VI

SUMMARY

The prey species composition of Great Blue Herons
foraging in the Coos Estuary is similar to that reported by
Krebs (1974) for herons at the mouth of the Fraser River,
Vancouver, British Columbia. The Staghorn Sculpin
(Leptocottus armatus) composed 28.2% of Coos Estuary herons'
observed diets, followed by an unidentified codlike species,
probably juvenile Lingcod (Ophidon elongatus). The bulk of
the remainder of the fish diet was composed of Flatfish
(Pleuronectiformes), especially the Starry Flounder
(Platichthys stellatus) (14.8%), surfperch (Embiotocids)
such as the Shiner Surfperch (Cymatogaster aggregata)
(14.1%), and Gunnels or Pholid type, especially the
Saddleback Gunnel (Pholis ornata) (13.9%). Foraging rates
for different species for solitarily foraging herons
differed significantly from those of socially foraging
herons in the much lower catch rate of pholids for solitary
herons, and the much lower catch rate of Staghorn Sculpins
taken by socially foraging Great Blue Herons. Solitary
herons also took significantly fewer per effort small
unidentified prey (probably Crangon and Heptacarpus spp.)

than did social herons.

Without knowing the concurrent distribution and densities of prey in areas where the heron foraging activities were observed, it is difficult to ascertain precisely why certain prey types were taken at higher rates by either socially or solitarily foraging herons. Given the obvious differences in the various prey morphologies and the suspected differences in their general behaviors, however, a study was conducted to determine if some specific prey behaviors might allow them to be more efficiently exploited by solitarily or socially foraging wading birds, as predicted by a geometric idealized prey behavior model. The flight responses of two of the major contributors to the Great Blue Heron's diet observed to have been taken at disparate rates by social and solitary herons, Staghorn Sculpins and Shiner Surfperch, were described in controlled laboratory experiments. Shiner Surfperch react to wading bird type disturbances with the predicted "bomb crater" response, with those closer to the disturbance reacting more strongly than those farther from the disturbance. After this initial reaction, a strong schooling instinct prevails, and the school will generally move away from the point of disturbance, unless compelled to remain by the presence of a refuge. In contrast, Staghorn Sculpins exhibit few predictable flight responses. There was no correlation between the strength of their reaction to the disturbance

(as gauged by flight distance) and their proximity to the disturbance. Though the percent responding did decrease as the disturbance distance increased, the variability in the flight response distances of those that did react indicates that disturbance facilitated feeding tactics employed by socially foraging wading birds would be an ineffective means of capturing this prey species. Furthermore, the sculpins general decrease in activity after encountering a heron disturbance would greatly increase search times for herons that may be dependant on some type of movement to detect these otherwise extremely cryptic prey.

Though resource distribution can undoubtedly select for a solitary or social foraging strategy in many species, care must be taken when applying these models to predators engaged in the pursuit of active and behaviorally sophisticated prey. In the case of Great Blue Herons foraging for prey as behaviorally well-adapted for avoiding predation as the Staghorn Sculpin, it seems particularly unwise to equate them as resource with nectar or grain. Prey tactics in response to predator disturbance may not only proximally influence predator tactics, but ultimately influence predator foraging strategy.

APPENDIX

QUANTIFICATION OF OF BENEFITS OF DISTURBANCE
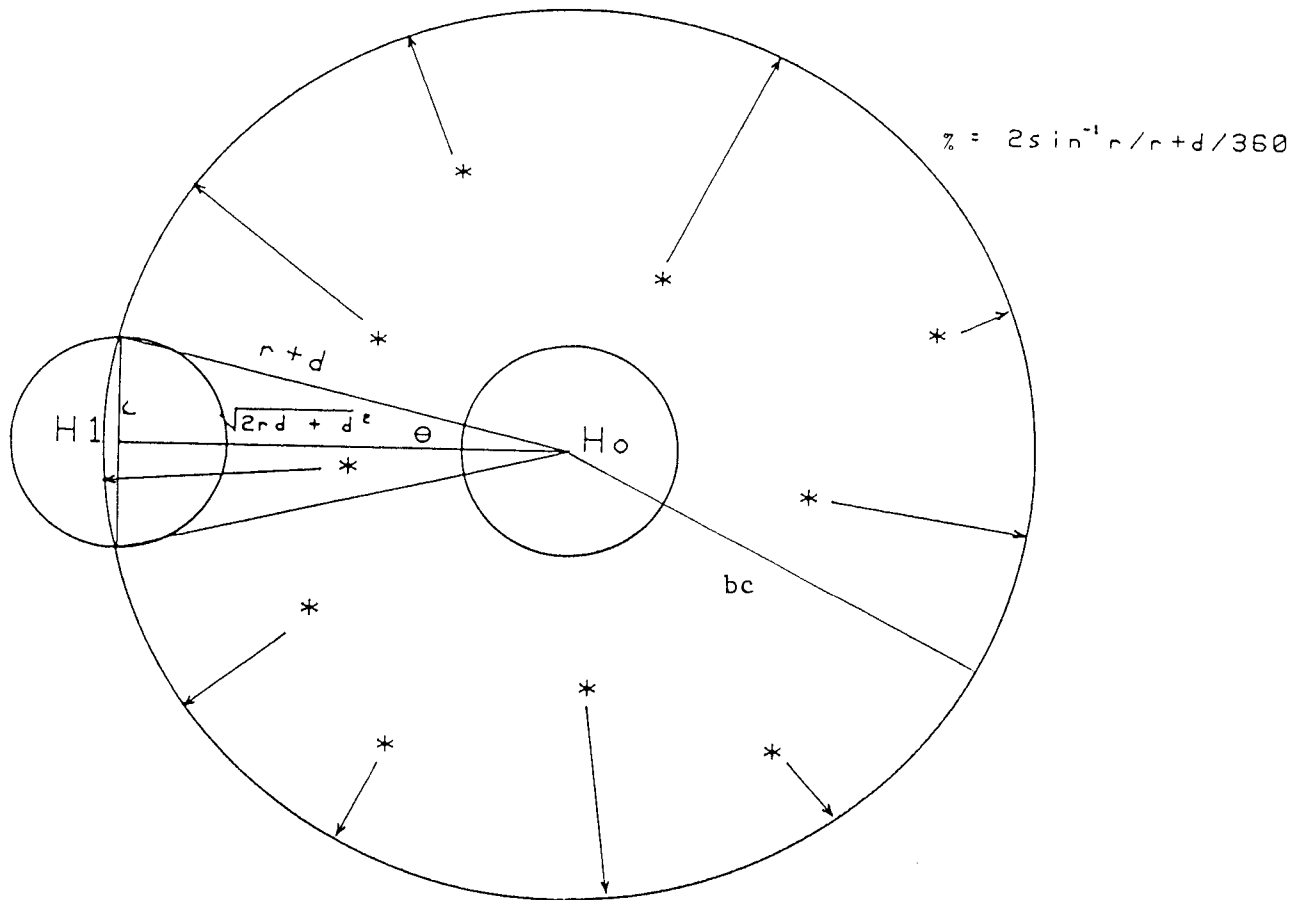
FACILITATED FORAGING

Figure 1. Probability of a wading bird (H1) encountering prey disturbed by another wading bird (Ho) in close proximity. The probability, as defined by the portion of the circle bc within the strike radius r of heron H1, can be described by the equation shown, where r = heron strike radius, and d = the flight distance of prey exhibiting "bomb crater" flight response.
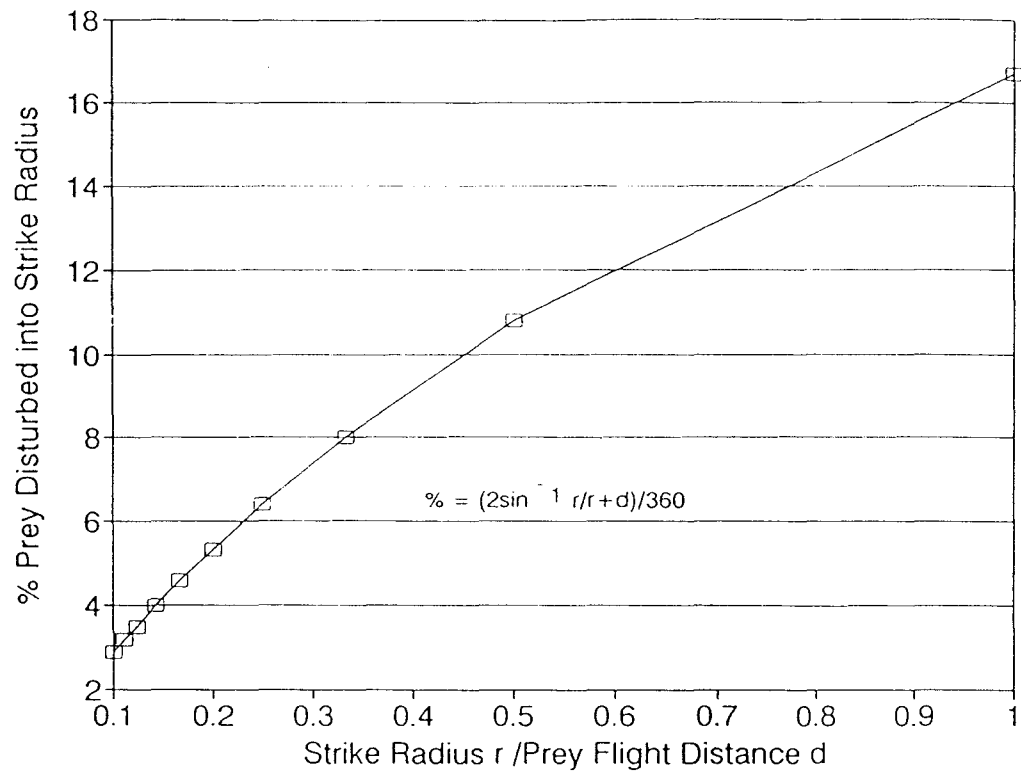
Figure 2. Function of the probability of encountering prey $[2(\sin^{-1}r/r+d)/360$ x100] as the ratio of strike radius to prey flight distance increases.

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