mosquitoes have been centered on its role in egg development. However, behavioral roles for ecdysone are known in other insects. In the desert locust, *Schistocerca gregaria*, the rise in ecdysone titer which occurs in conjunction with molting also acts on the central nervous system of the animal to suppress postecdysis locomotor activity (*11*). Locusts in this state enter a solitary phase thereby increasing the probability of successfully completing the molt. Whether ecdysone-induced inhibition of biting behavior is also characterized by changes in the central nervous system remains to be investigated.

Note added in proof: Klowden and Lea (*12*) have reported that an unidentified hemolymph-borne substance, present during egg development, inhibits host-seeking behavior in *Aedes aegypti*.

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References and Notes

1. A. N. Clements, *The Physiology of Mosquitoes* (Pergamon, New York, 1963), p. 270.
2. H. H. Hagedorn, J. D. O'Connor, M. S. Fuchs, B. Sage, D. A. Schlaeger, M. K. Bohn, *Proc. Natl. Acad. Sci. U.S.A.* **72**, 3255 (1975).
3. A. Spielman, personal communication. The ovaries are removed with a microhook made from a sharpened insect mounting pin. The mosquito is lightly anesthetized and immobilized. The hook is then used to make an incision beneath the sixth abdominal tergite. The ovary, which lies just under the insect tegument, is hooked and removed.
4. Injections were made with glass needles fabricated from capillary tubing and calibrated.
5. The hormone, ecdysterone (Calbiochem.), was dissolved in 2 percent ethanol in Lum's saline [P. T. M. Lum, *Ann. Entomol. Soc. Am.* **54**, 397 (1961)].
6. Cholesterol (Sigma, St. Louis) was suspended at a concentration of 5 μg/μl in 5 percent ethanol in Lum's saline.
7. The β-ecdysone (10 mg) was partially dissolved in 0.5 ml of 5 percent ethanol and pipetted onto a 1-g sugar cube.
8. C. L. Judson, *Biol. Bull. (Woods Hole, Mass.)* **133**, 369 (1964).
9. M. J. Klowden and A. O. Lea, *Am. J. Trop. Med. Hyg.* **27**, 827 (1978).
10. R. W. Gwadz, *J. Insect Physiol.* **15**, 2039 (1969).
11. P. T. Haskell and J. E. Moorhouse, *Nature (London)* **197**, 56 (1963).
12. M. J. Klowden and A. O. Lea, *J. Insect Physiol.*, in press.
13. I thank R. Gwadz for helpful discussion during the course of this investigation.

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Nest Guard Replacement in the Antarctic Fish *Harpagifer bispinis*: Possible Altruistic Behavior

Abstract. *Nesting biology of the Antarctic plunder fish,* Harpagifer bispinis *(Schneider), was examined at Arthur Harbor, Antarctic Peninsula, during the austral winter, 1975. Females prepare nest sites, spawn, and guard the eggs for 4 to 5 months, the longest guarded incubation period reported for any fish species. If this guard is removed, it is soon replaced by a conspecific, usually male. If the second guard is removed, a third replaces it. Guards are essential to ensure nest survival. Selfish or parental acts or acts of kinship or reciprocity do not adequately explain guard replacement. The act may be altruistic.*

True altruism occurs when an act is performed that benefits an unrelated individual to the detriment, defined in terms of personal fitness, of the donor who can expect neither immediate nor future repayment (*1*-*3*). To date, such acts have not been documented in natural populations, but debate surrounding their possibility remains active (*1*, *4*, *5*). Recent studies that have examined seemingly altruistic behavior in natural populations have indicated that the observed behavior could be explained without resort to true altruism (*3*, *6*). Here I report on apparent altruistic acts in the nesting behavior of *Harpagifer bispinis*, a small demersal fish found in shallow, rubble bottom coves along the Antarctic Peninsula (*7*). Females prepare nest sites in June and spawn from late June to mid-August in Arthur Harbor (64°46′S, 64°04′W), where this study was conducted (*8*). If undisturbed, the female remains on the nest (Fig. 1) until the eggs hatch 4 to 5 months later. This is the longest brooding period reported for any fish (*9*) but may be common among Antarctic species (*10*). The guard is necessary for egg survival since it protects the nest from egg predators and prevents a fungal growth that destroys all unguarded nests within 2 weeks (*8*). If the initial guard is removed, a second fish, usually male, assumes most guard responsibilities. If the second guard is removed, a third fish, also male, assumes guardianship.

When apparent altruistic acts, such as the above, are observed, one of several alternative hypotheses is generally invoked: (i) the act is primarily selfish and the apparent altruism is incidental; (ii) the act is parental; (iii) the act is one of kinship (*1*) in support of a closely related individual; (iv) the act is one of reciprocity (*2*); (v) the act is misdirected selfish or parental behavior (*11*); or (vi) the act is one of true altruism. Each hypothesis was tested in turn, although the tests were limited by laboratory and field conditions, time, and the vagaries of Antarctic weather. I observed social interactions among *H. bispinis* on 48 dives in Arthur Harbor and for 150 hours over a 7-month period among a population maintained in a tank (95 by 50 by 50 cm) in the laboratory at Palmer Station. Behavioral observations in the field were limited because fishes tend to conceal themselves under rocks and because observation dives were limited to 30 minutes. Nevertheless, activities of individual fishes could be observed on successive dives since each individual has a distinct color pattern. As a result of a series of five dives conducted between 15 August and 27 December 1975 in a small cove (0.1 ha), approximately 30 individuals and seven nests were observed. The seven nest guards remained on their respective nests throughout the observation period. The other fish roamed about the cove but were never observed on the mud bottom area that separated the cove from other rubble areas. Of the 27 fish observed on the initial dive, 18 were recorded on the final dive. Five of the 12 fish observed on subsequent dives were also present on the final dive. The greatest straight line distance traveled by an individual still in the study area was 15 m. Protected sites, namely crevices and crannies under and between rocks, were abundant in the cove.

In order to make more extensive observations and manipulations, eight fish were introduced into the laboratory tank, which had only four protected sites. Initially, a weak dominance was established in which two coequal males tended to dominate the other individuals during encounters involving food capture. Dominance with respect to site use was also observed on occasion. All fish tended to rove; no individual occupied a single site for more than 24 consecutive hours, and site sharing by three to five individuals was not uncommon. On 10 August, one female spawned and began to guard the resulting nest. Observations continued until 15 December.

The following six points must be considered.

1) Selfish acts increase the fitness of the individual performing the act without regard to possible secondary effects, either beneficial or detrimental, to another individual. If guard replacement were a selfish act, the benefit accrued must exceed the cost involved. In the field, no nest guard was displaced from its nest by another fish. These fish may benefit by obtaining a permanent protected site. However, any overhanging rock can

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serve as a protected site, and these are abundant in the rubble bottom coves where *H. bispinis* occurs (*8*). The nesting female in the laboratory was also never displaced. The continuous occupation of the nest site by the female appeared sufficient to keep all other fish away. On only one occasion was another fish found on the nest. The nest guard displayed (*8*) and nudged the offender off the nest. The nest guard continued to feed, and encounters with the coequal males decreased. Thus, in a population where a dominance is established, nest guards may benefit from an increased social status. This behavior may have resulted from the space- and food-limited situation created in the tank; similar limitations were not observed in the field (*12*). If individuals benefit from nesting, one would expect intense intraspecific competition for nests (*13*). Even in the limited conditions created in the laboratory, this rivalry was not observed. Laboratory fish did not consume eggs, nor were any found in the 237 stomachs of guards, nonguards, males, and females collected during the nesting season (*12*).

If experience that will aid replacements in later nesting activity is gained, the act must be regarded as selfish. To demonstrate this, demographic data over several years are necessary, but not available. However, if experience were important, replacements would be female since males are not involved in nest preparation or maintenance (*8*). Since replacements are usually male, the experience gained may be of little value.

Some risk is involved in nest guarding. Several potential predators occur sympatrically with *H. bispinis*. Marshall (*10*) reported that Weddell seals (*Leptonychotes weddelli*) captured during the spring fed upon *H. bispinis* eggs. Since demersal fish comprise a large part of this species' diet (*14*), the guard is also in danger of being consumed. Blue-eyed shags (*Phalacrocorax atriceps*) also feed heavily on demersal fishes (*15*). The feeding of these predators in areas where *H. bispinis* occurs has not been examined. Replacement guards expend some energy, although less than what is spent by the initial guard (*8*), in cleaning and defending the nest from egg predators. However, neither gains in status nor experience appear to offset the expense or risk of guarding, although none appear great.

2) Parental acts include those performed by the parent in the normal course of rearing young. In the strictest sense, these acts are selfish since they increase the inclusive fitness of the parent. Spawning was not observed, and therefore whether or not multiple spawning occurs in this species is not known. However, the number of eggs per nest corresponds to the number of ova per female, and all eggs develop uniformly and hatch within 4 days (*8*). No evidence exists that guard replacements were parents; but evidence does exist that they were not in some cases. Eighteen nests were marked in the field during the austral winter and spring (Table 1). The initial guards, all female, were removed, and a thorough search was made around each nest to identify all fish in the immediate area. On the next dive, a second guard was removed. In all 14 nests examined a second time, the replacement guard was male and was not a fish observed near the nest on the initial dive. From six of eight nests examined a third time, a second male guard was removed. Again, each fish was not one observed near the nest on a previous dive. If multiple fertilization occurs, replacement could be explained as a parental act. But if only parents guard nests, a nest removed from the field and introduced into a laboratory tank should remain unguarded. Replacement guards were observed within 12 hours on all three field nests placed in the laboratory tank where

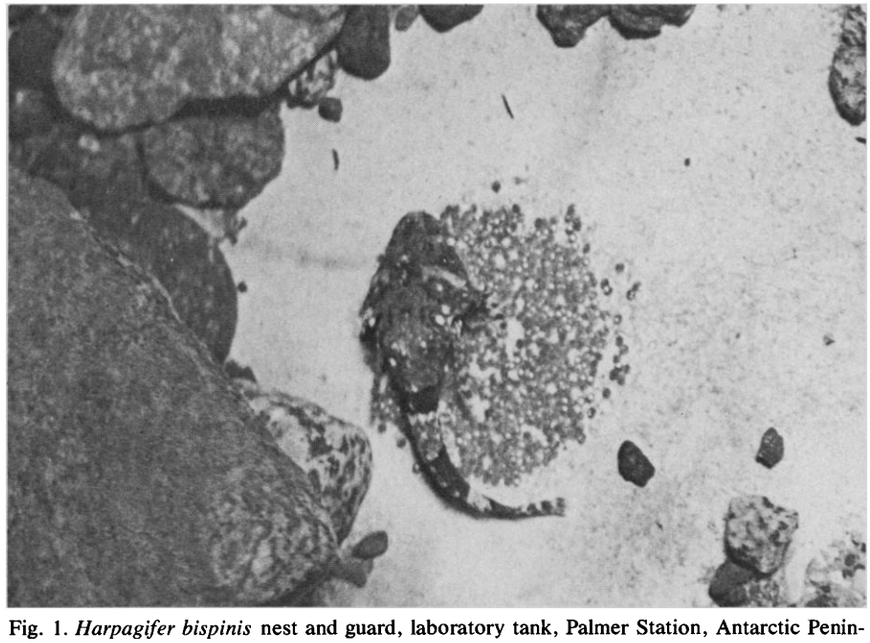

Fig. 1. *Harpagifer bispinis* nest and guard, laboratory tank, Palmer Station, Antarctic Peninsula, 1975.

Table 1. History of marked *H. bispinis*, Arthur Harbor, 1975. Abbreviations: M, male guard; F, female guard; U, unguarded; L, marker lost; H, hatched; D, dead.

No.	Depth (m)	Initial check		Second check		Third check		Fourth check	
		Date	Status of nest	Date	Status of nest	Date	Status of nest	Date	Status of nest
1	5	8/20	F	9/21	M	11/2	U*	12/26	D
2	7	8/20	F	9/21	M	12/3	M	12/26	H
3	7	8/20	F	9/21	M	12/3	M	12/26	H
4	7	8/20	F	9/21	M	12/3	L		
5	6	8/20	U	9/21	D†				
6	6	8/20	U	9/21	U	12/3	U	12/26	H‡
7	5	8/20	F	9/21	M	12/3	M	12/26	H
8	3	8/20	F	9/21	M	12/3	L		
9	2	9/19	F	10/22	L				
10	7	9/27	F	10/22	M	12/4	L		
11	12	9/29	F	12/3	M	12/14	M	12/27	H
12	6	10/17	F	11/2	M	12/27	M		
13	12	10/17	F	11/2	M	11/21	L		
14	18	10/17	F	11/2	M	12/27	L		
15	7	10/22	F	12/4	L				
16	7	10/22	F	12/4	M				
17	7	10/22	F	12/4	M				
18	9	10/29	F	12/3	M	12/14	M	12/27	H

*An urchin (*Sterechinus nuemayeri*) was found on the unguarded nest and removed. †Eggs were destroyed by a fungal growth. ‡This nest was laid under an algal frond (*Desmeristia anceps*) which brushed the eggs while swaying in the surge. The continuous movement of the algae probably allowed the eggs to survive to hatching.

the eight individuals were established. In all three cases a guard remained on each nest until it hatched. After the fish hatched, the guard abandoned the site. One of the replacements was a female that had not spawned. Thus it does not appear that guard replacement is solely parental. Again, these observations may be an artifact of the laboratory situation. In the field, the male parent may remain near the nest in order to accept guard responsibilities. This appears unlikely however, since replacements were never observed near the nest when the initial guard was removed.

3) Acts of kinship occur when an individual aids a closely related individual. Since acts of this nature essentially benefit the donor's own genes, they are not truly altruistic (*1*). The presence of closely related individuals in the study population does not seem likely. The sacfry are planktic and are carried by currents. Since they cannot swim well for at least 1 month after hatching and since the hatching is prolonged over a 3- to 4-day period (*8*), it is not likely that siblings will spend their planktic life or settle out together. Everson (*16*) reported that *H. bispinis* remain planktic for approximately 6 months, during which time it is unlikely that they ever become strong swimmers. The flattened, bullhead-like bodies and the sedentary behavior of the adults make extensive homing migrations unlikely. Also, kinship cannot be invoked to explain the ready acceptance of nests introduced into the laboratory tanks since tank fish were taken from areas several kilometers from the nest collection sites.

4) Acts of reciprocity occur when an individual aids a second individual who, at some later date, can be expected to assist the first (*2*). Reciprocity is not a likely explanation for guard replacement since the first guard is permanently removed from the population; replacements cannot expect reciprocation. Acts of reciprocity can be envisioned, however, if kinship and homing behavior are assumed. Here offspring of the initial guard could be expected to assist the replacement fish in later years. This, however, relies on two unlikely assumptions and adds to the complexity of an already complex situation.

5) Misdirected acts aid a beneficiary incidentally when a donor makes a mistake (*11*). Acts of this nature have been observed in a number of vertebrates, particularly involving brooding of nonkin (*17*). This explanation is generally invoked when an act is observed that cannot be explained readily by selfish, parental, kinship, or reciprocal behavior [see, for example (*4*, *5*)]. It necessarily requires speculation; in the case of *H. bispinis* one tract deals with the relative rates of predation. If natural predation on *H. bispinis* were low, the likelihood of any fish encountering an abandoned nest will be low. Since nest guards do leave their nests to feed, they must return to an abandoned nest. If topographical site cues are unimportant, then any abandoned nest, on the likelihood that it is its own, would be acceptable to the returning fish. Thus, what would appear to be an altruistic act to an observer would in fact be parental. This explanation is difficult to falsify since it requires the identification of the motivation behind the act. However, it relies upon some improbable assumptions. Site cues appear to be important. On one occasion, I altered a nest site by rearranging the surrounding rocks. On a dive 2 days later, another fish had assumed guardianship. The importance of predation remains to be examined.

6) The act may be altruistic. Hamilton (*1*) listed variables that affect the likelihood of altruism. They include the degree of relatedness, the cost to the donor, and the benefit to the recipient. Even at low degrees of relatedness, altruism is likely if the benefit/cost ratio (K) is fairly high. The ratio K is high when the recipient is in great need and when a small amount of aid is required from the donor. In *H. bispinis*, the recipients (eggs) benefit by being allowed to survive until hatching. Without a nest guard, a nest predator or fungal growth will destroy the nest (*8*). Replacement guards are less active and less persistent in nest defense (*8*), and no significant difference in feeding rate, growth, or condition between guards and nonguards was observed (*18*). Under these circumstances, altruism is possible.

When altruism is invoked, cheaters, in this case females who lay eggs and abandon them, must be considered. In this system, females are limited by their morphology, physiology, and the Antarctic environment. Fish are small and fecundity is low. Ova require more than 1 year to develop (*19*). Thus, although food is not limiting (*12*), digestion and assimilation rates may be too low to allow rapid ova development and multiple spawning.

Harpagifer bispinis populations fit Wilson's (*20*) trait-group model well. In Arthur Harbor, small groups (< 100 individuals) inhabit shallow, rubble bottom areas isolated from other groups by deep, mud-bottom areas. Similar situations exist in other areas along the peninsula as well. Since adults are relatively sedentary, and fry and fingerlings are planktic, *H. bispinis* fit Bell's "salmon" trait group (*21*). Under such conditions, Wilson and Bell conclude that altruistic behavior could establish itself and remain in a population. Planktic fry and fingerlings make it unlikely that only kin comprise the trait groups. Thus kin and trait-group selection are distinct in this case, and one of the other mechanisms suggested by Maynard Smith (*22*) must account for any resemblance among members of the trait group.

Additional information is necessary to finally explain this highly unusual behavior. Of particular importance are demographic and genetic studies of the individuals within the groups and differences and similarities between groups. Here I have examined each hypothesis with the available data, and these data favor altruistic behavior, although neither the selfish nor the misdirected behavior hypotheses can be completely discredited. As described, altruistic behavior is as parsimonious an explanation (*11*) as the alternatives; it appears likely in terms of simplicity and completeness, and merits further study.

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References and Notes

1. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).
2. R. L. Trivers, *Q. Rev. Biol.* **46**, 35 (1971).
3. H. W. Power, *Science* **189**, 142 (1975).
4. S. T. Emlen, *ibid.* **191**, 808 (1976); V. J. Konečni, *ibid.* **194**, 562 (1976); K. R. McKaye, *Am. Nat.* **111**, 301 (1977).
5. J. A. Coyne and J. J. Sohn, *Am. Nat.* **112**, 447 (1978).
6. P. W. Sherman, *Science* **197**, 1246 (1977); M. A. Staton, *Am. Nat.* **112**, 327 (1978).
7. H. H. DeWitt, "Coastal and deep-water benthic fishes of the Antarctic," *American Geographic Union Map Folio Series No. 15* (1971).
8. *Harpagifer bispinis*' nesting behavior is described in R. A. Daniels, *J. Fish Biol.* **12**, 465 (1978).
9. C. M. Breder and D. E. Rosen, *Modes of Reproduction in Fishes* (Natural History Press, Garden City, N.Y., 1966).
10. N. B. Marshall, *Evolution* **7**, 328 (1953); A. P. Andriashev, *Monogr. Biol.* **15**, 491 (1965).
11. G. C. Williams, *Adaptation and Natural Selection* (Princeton Univ. Press, Princeton, N.J., 1966).
12. R. A. Daniels, *Fish. Bull.*, in press.
13. S. Rohwer, *Am. Nat.* **112**, 429 (1978).
14. J. H. Dearborn, *J. Mammal.* **46**, 37 (1965).
15. R. P. Schlater and C. A. Moreno, *Ser. Cient. Inst. Antart. Chileno* **4**, 69 (1976).
16. I. Everson, *Br. Antarct. Surv. Bull.* **16**, 65 (1968).
17. For example, S. C. Kendiegh, Ill. *Biol. Monogr.* **22**, 178 (1952); R. D. Estes and J. Goddard, *J. Wildl. Manage.* **31**, 52 (1967); A. J. Ribbink, *Nature (London)* **267**, 243 (1977).
18. Mann-Whitney U tests on changes in fullness indices, mean standard lengths and condition factors, $P < .01$. Indices from W. E. Ricker, Ed. [*Methods for Assessment of Fish Production in Fresh Waters* (Blackwell, Oxford, 1968)].
19. This is true for other Antarctic fishes as well; see I. Everson, *Br. Antarct. Surv. Bull.* **23**, 81 (1970).
20. D. S. Wilson, *Am. Nat.* **111**, 157 (1977).
21. G. Bell, *ibid.* **112**, 389 (1978).
22. J. Maynard Smith, *Q. Rev. Biol.* **51**, 277 (1976).
23. Supported by NSF grants GV-31162 and OPP74-12139. I appreciate the valuable discussions with and ideas expressed by D. M. Baltz, T. E. DeLaca, H. W. Li, J. H. Lipps, D. F. Lott, W. Stockton, and S. K. Tanaka. D. Laine and W. Showers partnered the dives. I am also thankful for discussions with and editing by W. D. Hamilton, J. Monroe, P. B. Moyle, and D. S. Wilson.

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