

## SPITE AND ALTRUISM IN GULLS

In recent years, a controversy has developed in evolutionary biology concerning the existence of altruistic behavior in species other than *Homo sapiens* (Trivers 1971; Wilson 1975; Power 1975, 1976a, 1976b; Emlen 1976; Konecni 1976). Basically, as outlined in Power (1975), if true altruism is proven to exist, Darwin's (1859) theory of natural selection would be inadequate to account for all of evolution. This is because Darwin assumed that individual organisms should always act in their own self-interest, whereas altruistic behavior at least potentially reduces the fitness of an individual in order to increase the fitness of another individual.

Along with the controversy over altruism, there has developed a minor, related controversy concerning spiteful behavior in animals (Hamilton 1970, 1971; Wilson 1975). Spiteful behavior is best defined by Wilson (1975 p. 117) as "behavior that gains nothing, or may even diminish the fitness of the individual performing the act, but is definitely harmful to the fitness of another (presumably a conspecific)." In practice, spite may be difficult to distinguish from purely selfish behavior, which is one of the cornerstones of Darwinian natural selection. The criterion for spite must therefore be the high risk of personal injury to the individual performing the act relative to the potential gain.

I emphasize that, in describing behavior as either altruistic or spiteful, I am not implying anything about the psychological state of the individual performing the behavior. I only wish to characterize the potential effects of the act upon the fitness of the individual performing the act, and upon the fitness of the recipient of the behavior.

The link between spite and altruism is the controversial implication that the individual exhibiting such behavior lowers its personal fitness. Much of the controversy concerning supposed altruistic behavior has been resolved by Hamilton (1964), who defined the concept of "inclusive fitness," and by Maynard Smith's (1964) definition of "kin selection" based on "selection of families" as suggested by Darwin (1859). These concepts, which are best exemplified by the social insects (Wilson 1971), suggest that behavior which appears altruistic may in fact be selfish in an evolutionary sense if the behavior increases the fitness of relatives more than it decreases the fitness of the performer.

Some organisms, however, appear to show altruistic behavior under conditions where it would seem spurious to invoke kin selection. To account for such behavior within the bounds of Darwinian natural selection, Trivers (1971) suggested the concept of "reciprocal" altruism, where the individual acts of altruism are not generally risky and, in the long run, the organism will receive many more benefits (and presumably increase its fitness) from other organisms reciprocating, i.e., performing other altruistic acts in return. However, Trivers' best examples of such behavior were either interspecific (e.g., cleaning symbioses) or involved *Homo sapiens*. Unequivocal examples of reciprocal altruism between conspecifics appear to be extremely rare. In this paper I will provide some possible examples.

As a result of the apparent lack of strong supporting evidence, reciprocal

altruism remains a controversial concept. Part of this controversy may stem from the supposed ethical implications that acceptance of reciprocal altruism would hold for the behavior of *Homo sapiens*, and particularly from the suggestion that the ultimate causative factors of altruistic behavior in humans are selfish rather than selfless.

I describe here some behavior patterns that appear to be altruistic and others that appear to be spiteful in a group of colonial seabirds, the gulls (genus *Larus*). I will explore the selective forces that could have produced such behavior. Most of my examples will be taken from a 2-yr study on the western gull (*Larus occidentalis*) on Southeast Farallon Island, California (lat. 37°24' N, long. 123° W), and from a 2-yr study of the herring gull (*L. argentatus*) on Great Island, Newfoundland (lat. 47°11' N, long. 52°46' W).

#### METHODS

During the studies on both species, individual birds were recognized by noting identifiable characteristics, e.g., markings on bill or feathers, holes or tears in webs of feet. Several individuals were captured and color-ringed as well. The sex of individuals was determined by a combination of two methods. First, the role taken in courtship and copulation by recognizable individuals was noted, and second, during the initial field season of the western gull study 36 individuals were collected (15 males, 21 females). Before collecting them, I sexed most of these individuals in the field by using criteria such as larger overall size and larger and heavier bill in males. Males proved significantly larger in all measurements taken. There was no overlap between males and females in weight and in bill width and depth at the nares (Pierotti 1976).

Birds collected in the experiment described under stepmothering (see below) were included in the above sample. Each time I set out to collect an individual of a specific sex, I was successful in doing so. In the experiments described under adoption, I followed the method described in Coulter (1973), where chicks 1 or 2 days old were added to nests containing chicks of the same age.

Observations on both species were conducted from blinds during continuous watches lasting from 12–15 h. A 15–60 power spotting scope and 7 by 50 binoculars were used to facilitate recognition of individuals. Observations on both species were initiated in late April–early May and continued until late July–early August, so that the entire breeding season was monitored from courtship through fledging. All observations were carried out on known individuals (except where specifically noted), so that the subsequent histories of spiteful and altruistic individuals could be noted.

#### ALTRUISTIC BEHAVIOR

All of the altruistic behavior that I was able to observe in gulls involved the care of chicks. This behavior took three forms: (1) “stepmothering” (if the female of a pair died or disappeared, the male would remate and the new “stepmother” would

aid in the care of the offspring); (2) adoption of chicks; and (3) creching of chicks from several broods, which were fed and guarded by all parents indiscriminately.

*Stepmothering.*—To test whether or not individual parent birds could assume the entire burden of chick care, I removed one adult (in all, five females and two males) from each of seven western gull nests during the late stages of incubation or within a few days after hatching. All five male birds remated within 2 days, but the two females deserted their nests after trying to incubate their eggs independently for 3 or 4 days.

Without exception, the new female mates helped to raise the offspring of the previous mate. Three of the five females only attended, guarded, and fed young that had already hatched, but two new females actually helped to incubate the eggs laid by the previous mate. I captured both of these females, and neither showed any sign of brood patches, which indicated that they had not previously bred during that season. This eliminates the possibility of reproductive error, which was suggested by Power (1975) to explain similar behavior on the part of a female mountain bluebird (*Sialia currucoides*). In addition, these results cast doubt on Emlen's (1976) suggestion that Power's bluebirds did not behave in an altruistic manner because they were not in the proper hormonal state to begin parental care.

It is interesting that in both the western gull and the mountain bluebird only females helped to rear another individual's offspring. In the bluebird, out of 10 rematings observed by Power (1975) eight involved males who provided no aid to the nestlings of the females they joined. In the western gull, the two bereft females apparently could not induce a male to join them at their nests. I also observed another female, whose mate deserted her through natural causes, acquire another mate; but he did not aid her with her chicks, and they subsequently perished.

This difference between the sexes in response to an unpaired bird with offspring may provide an explanation for this altruistic behavior on the part of female gulls. On southeast Farallon Island competition for breeding space was very intense, and there may be a surplus of breeding-age females in the population of western gulls (Pierotti 1976). Thus, an unmated female that helps a male to raise his offspring may solidify a pair bond between them, and guarantee herself both a mate and a breeding site for subsequent years. Both females that were captured on the nest and color-banded remained with the male on that site for at least 2 yr after their initial appearance. This population of western gulls occupies its breeding territories for at least 9 mo a year (Pierotti 1976), and pairs may remain together for several years. Acquisition of a breeding territory complete with mate could be a compelling incentive for a female gull to behave altruistically, since she would probably increase her personal fitness with only a small personal cost. This would then be an example of reciprocal altruism.

*Adoption in the Western Gull.*—During studies of parental care and activity budgets of western gulls (Pierotti 1976), I artificially doubled several broods to six from the normal size of three. Every chick was accepted by the adults at the nests where they were placed. Similar experiments on the same population of western gulls by Coulter (1973), and on the glaucous-winged gull (*Larus glaucescens*) by Vermeer (1963) and Ward (1973) gave identical results; that is, all chicks were accepted.

Most parent birds cue to the nest or to the entire brood or clutch rather than to individual chicks (e.g., Tinbergen 1953). In gulls, however, there are two reasons for viewing adoption as unusual. (1) Gulls belong to a group of birds in which parental recognition of offspring generally occurs early in the chick's life. (2) I observed adoption to occur in gulls under natural conditions involving chicks up to 1 wk old.

Gulls belong to the group of birds that have seminidifugous offspring (Lack 1968). This means that the young, while behaviorally precocial, are unable to provide food for themselves. Most bird species have altricial (nidiculous) offspring which are restricted to the nest until they are nearly independent, so that it is virtually impossible for adoption to occur under normal conditions. Other species have fully precocial (nidifugous) offspring, which are capable of foraging for themselves immediately after hatching. Adoption in these species would require little or no extra effort upon the part of parent birds. Therefore, only in those species that have seminidifugous offspring would one predict that parents would evolve means of identifying their own young at a very early age, and this is true in most species with seminidifugous young that have been studied in detail (Buckley and Buckley 1972; Tschanz 1968). A few gull species that nest regularly in dense colonies (e.g., ring-billed gulls, *L. delawarensis*, Evans 1977) are known to recognize their own offspring within a few days after hatching, but even these species take longer to recognize their young than other species with seminidifugous offspring. It therefore seems curious that early recognition of chicks would not have been selected for in all gull species, and that, given the nearly universal clutch size of three eggs in gulls (all known exceptions have normal clutches of less than three), that gulls do not reject chicks in excess of this number, unless there has been some selective pressure to behave in such an altruistic manner.

I postpone discussion of the adaptive significance of adoption until after I consider creching behavior, since I feel that adoption and creching are probably different responses to the same general set of selective pressures.

*Creching in Herring Gulls.*—In creching, the young gather in large groups that are guarded by adults around the periphery of the group (Wilson 1975). In penguins and in terns, the young are recognized by their parents and are fed only by them (Thompson and Emlen 1969; Buckley and Buckley 1972). In herring gulls in Newfoundland, however, groups of young form, and their parents guard the group and may feed any chick, regardless of its parentage. I observed one group of six chicks from different nests on adjacent territories that was fed by at least four different adults from the two adjoining territories over a period of about 4 wk. There was no apparent attempt by any of these adult birds to feed any specific chick or group of chicks. Food was simply regurgitated onto the ground where any chick present could grab it. These chicks were fed in this manner until they were more than 6 wk old and nearly fledged, which is well after the time when herring gulls are said to be able to recognize their own young (Tinbergen 1953; Evans 1977).

John Lien (personal communication) and his associates have observed similar groupings of unfledged herring gull chicks on Red Island, Newfoundland. Lien suggests that the creching that he observed helped the adults to protect the young

from terrestrial predators, primarily rats (*Rattus* spp.). Great Island, where I observed creching, has no terrestrial predators, but ravens (*Corvus corax*) and great black-backed gulls (*L. marinus*) were observed to prey on young herring gulls. Also, this was the first year that large areas of this herring gull colony had ever been consistently disturbed by man.

Adoption and behavior that resembles creching have been reported in other species of gulls. Howell et al. (1974) reported an example of apparent altruistic behavior in the gray gull (*L. modestus*). This species breeds in the extreme heat of Chile's barren Atacama Desert, where heatstroke is apparently the major cause of chick mortality. Consequently, the adults brood the chicks by standing over the nest scrape, shading it and any chicks in the scrape. Adults attack any chick, including their own, that is out of the nest scrape and approaches it. However, their aggression is extremely ritualized and of low intensity, and chicks easily avert it by assuming a submissive posture (Howell et al. 1974). When a chick succeeds in reaching the scrape the behavior of the adult changes from aggression to broodiness, and it will brood, and even feed, any chick in its nest. This is apparently independent of the age of the chick; which is surprising, since most gulls, including those that adopt regularly, learn to distinguish their own chicks when these are anywhere from 10–15-days old (Beer 1970).

Roberts (1900) described mass adoptions in Franklin's gull (*L. pipixcan*). This species nests in marshes, and young birds frequently swim or are blown away from their nests, which are floating platforms of reeds. This displacement of young is especially frequent when the marshes are flooded and many nests float free of their moorings. Under these circumstances any chick that is able to climb onto a nest platform is accepted by the resident adults. According to Roberts, the adults may even retrieve these lost young birds from the water until they have as many as a dozen chicks in the nest. These adults then brood and continue to care for these chicks. Burger (1974) has substantiated some of Roberts' observations by demonstrating that Franklin's gulls will accept any chick for adoption that is less than 14-days old, at which time the chicks are able to find their way back to their own nests if they become separated.

All of these examples show that, for at least several days after hatching, several gull species cannot recognize their own offspring, or, if they can discriminate, are willing to adopt strange chicks. These results suggest two possible hypotheses. (1) Under certain sets of conditions (especially when extrinsic factors are important in causing chick mortality), chicks have evolved to be difficult to recognize more rapidly than adults evolved the capacity to recognize them, which could be considered an example of "parent-offspring conflict" (Trivers 1974), or (2) some form of reciprocal altruism exists in nearly all species of larid gulls, and this altruistic behavior is most evident where conditions for rearing chicks are regularly adverse. I explore these hypotheses further in the discussion section.

#### SPITEFUL BEHAVIOR

In addition to the altruistic behavior evident in some gull species, spiteful behavior has also been observed in at least three species of gull. Establishing the

TABLE 1  
COMPARISON OF PIRATES AND NONPIRATES

	NO. OF CHICKS FLEDGED				ALL CHICKS FLEDGED
	0	1	2	3	
<b>1973</b>					
Pirates ( $N = 11$ )*	1	8	2	0	0
Nonpirates ( $N = 15$ )	0	3	8	4	7
<b>1974</b>					
Pirates ( $N = 9$ )†	3	3	0	3	4
Nonpirates ( $N = 16$ )	0	5	2	9‡	12
<b>Totals</b>					
Pirates ( $N = 20$ )§	4	11	2	3	4
Nonpirates ( $N = 31$ )	0	8	10	13	19

\* Probability less than .004 by Fisher's exact test.

† No full-time pirates in 1974.

‡ Includes one pair that fledged four chicks (two adopted).

§ Probability less than .005 by  $\chi^2$  test.

existence of spite is, in some ways, even more problematic than establishing the existence of altruism, since spite involves a decrease (or at least a potential decrease) in the fitness of both the perpetrator and the recipient of the act. In addition, spiteful behavior often appears to result from some form of "injury" which has been done to the spiteful individual.

The spiteful behavior that I observed was, like the altruistic behavior, directed almost exclusively at chicks and was always performed by male gulls. Observed spiteful behavior took two forms: (1) conspecific piracy (cleptoparasitism) directed at neighboring birds, and (2) attacks on fledged or nearly fledged chicks.

**Piracy.**—Piracy, or cleptoparasitism, is a common foraging strategy of several species of seabirds (Ashmole 1971). However, it is generally directed at members of other species (Meinertzhagen 1959; Nettleship 1972). When observed between conspecifics, it usually involves independent birds squabbling over a limited food resource away from the breeding grounds (Hatch 1970, 1975). Among western gulls on southeast Farallon Island it was a major, if not the sole, foraging method of some adult males (Pierotti 1976). Piracy was more common in 1973, when the food supply was poor, than in 1974, when the food supply was more normal. Pairs with pirating males had significantly lower reproductive success than did other pairs. However, an examination of the timing of chick mortality showed that males that became pirates had lost all, or most of their offspring as eggs or in the first few days after hatching.

Data collected in 1973 (a poor food year) and 1974 (a good year) demonstrate that food supply can apparently affect the occurrence of piracy (table 1). In 1973 no pirate fledged three chicks, and all pirates lost chicks soon after hatching. In comparison, of the 15 nonpirates, eight fledged two chicks and four fledged all three. In 1974 no males were full-time pirates, and only nine were pirates even part of the time. In both 1973 and 1974 only pirates failed to fledge any chicks; in 1974, 75% of the nonpirates, but less than 50% of the pirates, fledged all of the chicks that they hatched.

TABLE 2  
STRATEGY SWITCHERS

CHICKS	PIRATE 1973	NONPIRATE 1974	NONPIRATE 1973-PIRATE 1974	
			1973	1974
Male no. 10 .....	1	4	...	...
Male no. 22 .....	1	3	...	...
Male no. 38 .....	0	1	...	...
Male no. 37 .....	2	1	...	...
Male no. 14 .....	...	...	2	0
Male no. 42 .....	...	...	3	1

The individuals that indicated the most about the causes of piracy, however, were the strategy switchers: birds that were pirates in 1973 but not in 1974 and vice versa (table 2). Of the four birds that abandoned piracy in 1974, three had increases in the number of chicks fledged, and the fourth remained constant. In contrast, the two males that took up piracy part time in 1974 both fledged fewer chicks than in 1973.

Conspecific piracy can be extremely disruptive, especially in a colony as dense as that on the Farallones. The sequence of events involved in piracy began with the return of a bird to its nest, and the regurgitation of food to its young. A neighboring male (sometimes several) would dive in and attempt to steal the food. This usually resulted in a struggle between the pirate or pirates, one or both of the parents, and the chicks for the food item. Serious fights resulted, and both adults and chicks sustained injuries. Out of 26 nests followed in 1973, 11 had chicks with injuries that resulted initially from attempted piracies. These included two chicks with broken or dislocated wings and one with a broken leg. Each of these three chicks died of starvation after their parents left the colony when their siblings had fledged. Adults also sustained injuries from fights during attempted piracies, including serious cuts, primaries torn out, and the apparent loss of an eye. A pirate male in 1973 sustained a broken or dislocated lower mandible that stuck out at an angle from his upper jaw. Since he neither returned to his territory nor was observed elsewhere on the colony in 1974 and 1975, this injury may have been responsible for his death.

Piracy clearly can be an inefficient and dangerous method of foraging. There are, however, two possible benefits of piracy. (1) A pirate need not leave the vicinity of his territory to obtain some food, therefore he can protect his surviving offspring (if he has any), and (2) pirates may lower the survival chances of their victim's offspring. In addition to causing injuries to chicks, the pirate also denies them food. Chicks that are hungry have been observed to wander about their territories more widely than well-fed offspring (Hunt and McLoon 1975). This subjects chicks to a greater risk of attack. Thus, a major selective force for piratical behavior may be that it reduces the breeding success of the pirate's competitors, and also reduces the competition that the pirate's own surviving offspring (if any) may face in the crucial first few weeks after becoming inde-

TABLE 3  
TOTAL BREEDING SUCCESS, PIRATES VERSUS NONPIRATES

	TOTAL NO. OF FLEDGED CHICKS (1973-1974)						
	0	1*	2†	3	4‡	5§	6
Pirates .....	0	2	2	0	2	1	0
Nonpirates .....	0	0	2	2	2	5	2

\* Includes no. 38 (table 2).

† Includes no. 14.

‡ Includes no. 37, 42, 22.

§ Includes no. 10.

pendent. Since pirates had lower breeding success than nonpirates over two seasons (table 3), it might particularly benefit these less successful males to reduce the number of fledged chicks in the total population.

*Attacks on chicks.*—I have observed adults of both the western gull and the herring gull attacking fledged young either flying or roosting well away from the territory of the adult performing the attack. Most investigators that have observed adult gulls attacking chicks have attributed this behavior to territorial defense (e.g., Hunt and Hunt 1976); yet, I observed that attacks directed at fledged chicks were far more persistent and intense than those directed at intruding adults. Since chicks probably cannot seriously threaten the territory of an adult, it seems likely that a spiteful component is involved. I have never seen an adult gull eat any portion of a conspecific chick that it had killed when the chick was more than 1-wk old, so food does not seem to have been a motivating factor in these attacks. The purpose of attacks on flying or roosting chicks can only be to kill or injure the offspring of other gulls.

Davis and Dunn (1976) observed apparent spiteful behavior in lesser black-backed gulls (*Larus fuscus*) on Skokholm Island, Wales. They found a high incidence of conspecific predation upon eggs and small chicks, mostly by males that had recently lost their eggs or chicks to another neighboring gull. Thus, a sort of "domino effect" was created: When one bird stole an egg or a chick, the victimized father then stole another pair's egg or chick, and so on. In some areas of their study plots, Davis and Dunn found a chick mortality of greater than 50% due to this predation. The benefits of such behavior to a bird that loses some young by accident are obvious. Davis and Dunn (1976, p. 72) note that . . . "in terms of gene frequency, any individual losing its own progeny still stands to gain some selective advantage by eliminating the progeny of conspecifics." This same argument could be extended to explain the phenomenon of conspecific piracy as well.

#### DISCUSSION

Gulls exhibit what appear to be both altruistic and spiteful behavior within the same species, the same population, and sometimes the same individual (e.g., male

no. 10 in table 2). I believe that this reflects the varying ecological conditions to which gulls must adapt. Gulls are opportunistic generalists, both as species and as individuals, and may have evolved as marginal populations, forced into less favorable habitats by more specialized species of seabirds. As seabirds go, gulls appear to be an *r*-selected group of species, laying three eggs while most seabird species lay only one (Lack 1968). Consequently, compared with other seabird species, gulls have a high potential rate of population increase. Gull populations are therefore probably strongly affected by fluctuations in food supply (Hunt and Hunt 1976) and some exogenous factors such as weather and changes in water level (see Ludwig 1974 for such an example). Most gull species then probably exist under "boom or bust" conditions, where intraspecific competition is either severe or virtually nonexistent. Under conditions where competition is nonexistent, there could even be selection for reciprocal altruism, since this might raise the mean fitness of individuals. However, when intraspecific competition is severe, there could also be selection for spiteful behavior directed towards conspecifics and their offspring.

In recent times man has had a profound effect upon the size of gull populations. The near extermination of several species of marine mammals and the overexploitation of populations of large piscivorous fish has probably reduced competition in the upper trophic levels of the marine environment, and the availability of human garbage as a food source for young gulls has allowed gull populations to reach unprecedented highs (Vermeer 1963; Kadlec and Drury 1968; Ward 1973; Graham 1975).

As gull population sizes have increased, so has the density at nearly all major nesting colonies (Kadlec and Drury 1968). Thus, gulls are experiencing increased intraspecific competition (at least for space) during a time of abundance. This combination of factors could produce the tendency in gulls to behave both altruistically (there is abundant food, so many young might be raised) and spitefully (more individuals are competing for limited nesting space). There exists also the possibility that some or all of the spiteful behavior might be pathological, as appears to be the case in laboratory rats, where such nonadaptive behaviors as mothers killing their own young have been observed to occur with severe crowding (Calhoun 1952).

It is worth noting that in gull populations that have not been greatly affected by human activities, such as the gray gull (Howell et al. 1974), altruistic behavior occurs but spite appears to be absent. These species nest in habitats that are regularly adverse for chicks, such as the desert, or are unpredictable, such as marshes which may flood or drain (Burger 1974). Under such conditions chicks may have evolved to be indistinguishable (at least to their parents). This could create a conflict of interests between the adult (which will always be better off if it can recognize its own offspring), and the chick (which could benefit a great deal if it can obtain care from adults other than its parents, especially if it becomes separated from them). However, if the cost to the adult is small this system should evolve with adults not bothering to distinguish between offspring. This would also lead to altruistic behavior on the part of adults.

In conclusion, gulls apparently behave in both an altruistic and a spiteful

manner. These behaviors, however, are evidently labile and expressed to different degrees in different environments.

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#### STABILIZATION OF A PREDATOR-PREY EQUILIBRIUM BY THE ADDITION OF A SECOND "KEYSTONE" VICTIM

The diversity-stability question has recently been the subject of renewed interest. While randomly constructed communities may decrease in stability with increasing size (May 1976), it is clear that complex communities do persist. This suggests that there may be ways of assembling large communities so that stability will be maintained. This note illustrates one means by which an unstable predator-victim community can be stabilized by the addition of a second "keystone" victim species. Stability analysis of a graphical system closely follows Rosenzweig's three-trophic-level analysis (1973). Graphical analysis of this sort is robust because the analysis is not limited to specific functions or small areas around the equilibrium point, but can be applied to equilibria occurring in large regions of the state space.

An example of two-species predator-victim isoclines is shown in figure 1. The

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