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COSTS OF ADOPTION IN WESTERN GULLS¹

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Key words: *Chick adoption, Western Gulls, Larus occidentalis.*

Naturally occurring chick adoptions have been noted in several species of gulls (reviewed in Evans 1980; see Holley 1984, Wittenberger and Hunt 1985), including the Western Gull, *Larus occidentalis* (Hunt and Hunt 1975, Pierotti 1980). Several hypotheses have been proposed to consider why adoptions occur regularly at certain nesting colonies. These include strategies for chick survival (Graves and Whiten 1980, Hébert 1985, Pierotti and Murphy 1985), reciprocal and/or weak altruism (Pierotti 1980, 1982; Pierotti and Murphy 1985; see Waltz 1981), and increased numbers of "mistakes" by adults nesting in high densities (Holley 1981, 1984). All of these hypotheses are based on the premise that adoption is maladaptive to foster parents (i.e., adoption reduces their inclusive fitness). Few data are available to support this premise. In this paper, we document additional cases of chick adoption in Western Gulls on Southeast Farallon Island (SEFI), California, and examine costs of adoption to foster parents.

About 25,000 Western Gulls nest on SEFI (Ainley and Lewis 1974). Various aspects of the breeding biology, behavior, and nesting habitat of the Western Gull on SEFI have been described by Coulter (1973, 1977), Pierotti (1980, 1981), Hand (1981), and Spear (1981, 1986), and Pen-

niman, Coulter, and Spear (unpubl.). Since 1971, the Point Reyes Bird Observatory (PRBO) has monitored plots of nests for breeding productivity and banded about 2,000 chicks (with a metal USFWS band and a plastic color band) each year. In 1978 and 1979, LBS monitored 141 and 226 nests where at least one mate was banded and of known age. Nests were visited every second day during the egg and early chick period. Eggs were marked in order of laying; chicks were dyed (picric acid) by hatching order and banded with individually color-taped bands when 10 days old. After banding until fledging, chicks were observed every few days with a telescope from vantage points (<50 m away). In 1980 to 1984, PRBO monitored 55, 96, 106, 100, and 90 nests in 3 plots each year. A few adults in each plot were banded. Plots were not entered and nests were observed daily from egg laying to fledging using binoculars or a telescope from vantage points and blinds above plots (<50 m away). Neither eggs nor chicks were marked, although the directions and distances of each brood's movement away from nest sites were mapped to assist in locating specific broods between days.

For nests monitored by LBS, adoptions were detected by the addition of an undyed chick to the dyed brood. Adopted chicks were dyed and/or banded individually. For nests monitored by PRBO, adoptions were detected by an increase in the number of chicks known to be at the nest or brood site on the previous day (see Holley 1981). In some cases, adopted chicks were larger or colored differently than foster parents' own chicks, which facilitated their identification. All adopted chicks maintained con-

¹ Received 3 July 1985. Final acceptance 10 January 1986.

TABLE 1. Chick adoptions by Western Gulls on Southeast Farallon Island, California, 1978 to 1984.

| Adoption No. | Nest visited | Year | Sex and age (yrs) of foster parents ¹ | Clutch size | Eggs hatched | No. and age (days, d) of chicks at time of adoption ² | | No. of chicks fledged | |
|-----------------|--------------|------|--|-------------|----------------|--|-----------|-----------------------|---------|
| | | | | | | Parents' own | Adopted | Parents' own | Adopted |
| 1 | Yes | 1979 | M 8 F UK | 3 | 0 ³ | 3, eggs | 1, 3-6d | 0 | 1 |
| 2 | No | 1983 | M UK F UK | 3 | 0 ³ | 3, eggs | 1, 4-6d | 0 | 1 |
| 3 | No | 1984 | M 6 F UK | 2 | 2 | 2, 1-4d | 1, 7d | 0 | 1 |
| 4 | Yes | 1978 | M 4 F UK | 3 | 2 | 2, 1-5d | 1, 10d | 0 | 1 |
| 5 | Yes | 1978 | M 5 F UK | 3 | 2 | 2, 1-5d | 1, 6-8d | 0 | 0 |
| 6 | Yes | 1978 | M 6 F UK | 3 | 3 | 3, 2-6d | 1, 6d | 2 | 0 |
| 7 | No | 1984 | M UK F UK | 3 | 3 | 3, 6-10d | 1, 5d | 3 | 1 |
| 8 ⁴ | No | 1982 | M UK F UK | 3 | 3 | 3, 12-15d | 1, 12-15d | 3 | 1 |
| 9 ⁴ | No | 1983 | M UK F UK | 2 | 2 | 2, 13-14d | 2, 13-14d | 2 | 1 |
| 10 | No | 1983 | M UK F 8 | 3 | 3 | 2, 21-23d | 2, 21-23d | 0 | 0 |
| 11 ⁵ | Yes | 1979 | M 3 | 0 | 0 | 0 | 1, 40-60d | 0 | 1 |

¹ Foster parents were sexed (F = female, M = male) by observing copulations, courtship feedings, and size differences (see Pierotti 1981; Spear 1981, 1986). UK = unknown age (unbanded in adult plumage).

² Ages of foster parents' own chicks were determined from hatching dates while ages of adopted chicks were determined by their size (except Nos. 2 and 3 where adopted chicks came from adjacent nests that also were being monitored).

³ Eggs were abandoned after adoption.

⁴ Both Nos. 8 and 9 occurred at the same site in different years.

⁵ This adoption involved an unpaired, subadult male that had not bred in 1979 (see text).

tinuous associations with foster parents' broods and received food and protection from foster parents.

Between 1978 and 1984, 11 adoptions were recorded in 5 of the 7 years (Table 1); 3, 2, 0, 0, 1, 3, and 2 adoptions were recorded in successive years. Adoptions occurred at 2.1, 0.9, 0, 0, 0.9, 3.0, and 2.2% of nests monitored per year, respectively. In most cases, the locations of adoptions were separated widely in varying types of nesting habitat, including flat and sloping terrain, but were mainly in areas of low vegetative cover. All except one occurred away from paths and other heavily visited areas.

Adoptions by adults that were incubating (Nos. 1, 2) or caring for small (<6-day-old) chicks (Nos. 3 to 6) occurred when adults generally lack the ability to recognize their young (reviewed in Evans 1980; see Pierotti 1980). Because small chicks are localized at the nest site (Noseworthy and Lien 1976) and usually are killed when away from their natal area, it would be expected that small adopted chicks tend to originate from adjacent nests (see Graves and Whiten 1980). In adoption No. 2, the chick presumably fell during high winds into the nest of its foster parents from a nest on a ledge 1.2 m above it. In adoption No. 3, the adopted chick also presumably came from an adjacent "uphill" nest. In both cases, an appropriately sized chick was missing from the neighboring nest on the same day the adopted chick was first noted in the foster parents' nest. In 3 of 4 adoptions by adults with small chicks (Nos. 4 to 6; not No. 3), the nest was surrounded by rocks up to 1 m high. In this habitat, the vision of foster parents was obstructed and chicks probably could enter nests without being detected.

Egg abandonment followed adoptions Nos. 1 and 2, as has been found elsewhere (Beer 1966, Kadlec et al. 1969, Graves and Whiten 1980). The adopted chick probably stimulated foster parents to switch from incubating to chick-tending behavior (Impekoven 1973). In adoption No. 2, the adopted chick was fed on the first day of adoption. These adoptions probably were facilitated by occurring late in the incubation period (see Tinbergen 1960, Miller

1972). In adoption No. 1, eggs were pipped; in adoption No. 2, eggs were due to hatch in four days. In adoptions Nos. 3 to 5, the addition of the single adopted chick merely produced a full brood size of three chicks. Adopted chicks, however, were larger than foster parents' own chicks and were observed to usurp the dominant feeding position. This probably caused or escalated the death of smaller siblings, which occurred shortly thereafter. Similar conditions normally promote brood reduction at this time (Coulter 1973, 1977; Hunt and Hunt 1975; Braun and Hunt 1983). All of the foster parents' own small chicks that did not fledge died on their territories and were not adopted elsewhere (see Holley 1984).

Adoptions by adults with large (>6-day-old) chicks (Nos. 7-10) occurred when adults generally can "respond selectively to" if not recognize their own chicks (Miller and Emlen 1975, Beer 1979, Evans 1980). Because all of these adoptions occurred in PRBO study plots, we were able to determine the origin of adopted chicks. In adoptions Nos. 8 to 10, adopted chicks originated from more than one to three territories away while in adoption No. 7, the adopted chick was from an adjacent territory. All adoptions of large chicks resulted in enlarged broods of four chicks whether one or two chicks were adopted. Only in adoption No. 10 had foster parents lost a chick prior to adoption. These adopted chicks were either the same size as (Nos. 8 to 10), or smaller than (No. 7), foster parents' own chicks. Enlarged broods fed together without any chicks obviously feeding more than other chicks. This probably led to survival of both the foster parents' own and the adopted chicks. Similar conditions naturally result after the period of brood reduction, where differences in sibling sizes, caused by differing egg sizes, hatching dates, and feeding rates of small chicks are diminished and most chicks survive (Coulter 1973, 1977, 1980). Only one of the large chicks that did not fledge in adoption No. 10 died on its territory. Why other chicks disappeared in Nos. 9 and 10 was not determined.

The adoption of a large chick by a subadult male (No.

TABLE 2. Success of foster parents at raising their own and adopted chicks.¹

| Stage of foster parents' nest at time of adoption | No. nests | Foster parents' own chicks | | | Adopted chicks | | Overall |
|---|-----------|----------------------------|--------------------|-------------------------|----------------|--------------------|--------------------|
| | | % fledging success | % sites successful | No. chicks fledged/site | % fledged | % sites successful | % sites successful |
| Eggs | 2 | 0 | 0 | 0.0 | 100 | 100 | 100 |
| Small chicks (<6 d) | 4 | 22 | 25 | 0.5 | 50 | 50 | 75 |
| Large chicks (>6 d) ² | 4 | 73 | 75 | 2.0 | 50 | 75 | 75 |
| Combined ² | 10 | 38 | 40 | 1.0 | 58 | 70 | 80 |

¹ Fledging success = chicks fledged/eggs hatched (including eggs pipped and near hatching in adoptions Nos. 1 and 2); sites successful = sites where adults fledged one chick (data from Table 1).

² Excludes adoption No. 11 by a subadult.

11) requires detailed documentation. This is the first recorded instance of adoption by a subadult gull. Only one other instance of adoption by a pair of adults without eggs or chicks has been noted (Holley 1981). Between 23 and 25 June 1979, a banded pair of four-year-old birds hatched their two-egg clutch. The banded second chick died on their territory in late July. In early August, the parents had dispersed from the colony, leaving the first chick before it could fly. This banded chick was observed roaming as much as 150 m from its territory. On 13 August, LBS first observed a banded three-year-old (subadult) male on the territory of the chick's parents and subsequently observed the subadult (by reading its band number with a telescope) with the chick through early September. On 9 September, the subadult was observed feeding the chick at the same location. The chick appeared very healthy in September and presumably dispersed from the colony (when it was at least 80 days old). In May 1979, LBS had observed the subadult at several locations in the colony as well as in a roosting group of nonbreeders. In June, he was seen in the vicinity (<100 m) of the territory where he later adopted the chick but never obtained a territory and certainly did not breed in 1979. After the adopted chick dispersed, the subadult continued to occupy the territory almost every evening through the fall of 1979. When other Western Gulls reoccupied territories in January 1980, LBS observed the subadult (now in adult plumage) fighting with two different males on the same territory. One fight involved the banded father of the adopted chick and the other involved an unbanded male, sexed by size (Pierotti 1981, Spear 1981). The young male won both fights. By 7 March 1980, he had paired and was occupying the site with his mate. He has bred at this site every year since (1980 to 1985).

When all adoptions are considered together, they caused reduced survival of foster parents' chicks. Only 38% of parents' own chicks fledged (Table 2) compared to the overall mean of 73% (for nests monitored by PRBO from 1971–1983 [Penniman et al., unpubl.]). However, reduced survival of foster parents' chicks occurred only in adoptions by adults incubating eggs or caring for small chicks where 13% of the eggs or chicks fledged (also see Graves and Whiten 1980). In contrast, adults caring for large chicks fledged 72% of their own chicks following adoption; this was a similar success rate to the overall mean. Hunt and Hunt (1975) and Holley (1981) also noted that adoptions of large chicks did not reduce fledging success in the original brood, even when this produced enlarged broods of up to six chicks. Nevertheless, adoptions of large chicks may have reduced postfledging survival of foster parents' own chicks through lowered growth rates and fledging weights, which can occur in enlarged broods (Nisbet and Drury 1972, Parsons et al. 1976; but see Coulter 1977, Harris and Rothery 1985). Since 58% of adopted chicks fledged, costs of adoption to foster parents included the propagation of competing genotypes (see also Graves and Whiten 1980, Holley 1981). LBS observed two of three banded adopted chicks that fledged (Nos. 1, 4; not No. 11), more than two years later. One of these birds (No. 1)

eventually bred on SEFI, near the location of the foster parents' nest.

Our data only support the premise that adoption is maladaptive to foster parents with eggs or small chicks (see Graves and Whiten 1980), at least in the year it occurs. Foster parents fledged at least one chick (including adopted chicks) in 80% of sites (Table 2), similar to the overall mean of 73% for nests monitored by PRBO (Penniman et al., unpubl.). Banded foster parents also returned and nested at the same site the following year in four of five cases (Nos. 1, 4, 5, 10; not No. 6) where this was checked. Thus, decreased breeding success due to adoption by adults with eggs or small chicks probably did not affect site tenacity (see Ollason and Dunnet 1978, Oring et al. 1983). The adoption of a large chick by the subadult, on the other hand, indicates that benefits can be gained. Through adoption, the subadult gained site-specific experience which probably assisted in the later acquisition of the territory (see Jamieson and Zwickel 1983). Whether other possible benefits to foster parents resulted from adoption was not determined. However, only 50% of foster parents with small chicks fledged adopted chicks (Table 2), despite adopted chicks being larger than, and competing with, two to three other chicks. In comparison, 75% of foster parents with large chicks fledged adopted chicks despite adopted chicks being the same size as, and competing with, three other chicks. Also, foster parents with large chicks fledged more of their own chicks per site than did parents without adopted chicks (2.0 vs. 1.5 chicks per site, respectively), and some were able to fledge enlarged broods (adoptions Nos. 7 and 8). These results suggest that foster parents with large chicks (late adopters) were of higher quality than foster parents with eggs or small chicks (early adopters). Since late adopters incur lower costs than early adopters, they are more likely to gain possible benefits from adoption (see Waltz 1981, Pierotti 1982).

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RANGE USE BY WINTERING ROUGH-LEGGED HAWKS IN SOUTHEASTERN IDAHO¹

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Key words: *Rough-legged Hawk*; *Buteo lagopus*; home range, range use, range fidelity, migration.

Rough-legged Hawks (*Buteo lagopus*) are the most numerous raptors, both as migrants and winter residents, in many areas of the western United States (Bock and Lep-

then 1976). Information on the winter ecology of this species, however, is incomplete. Descriptions of the movements and ranges of Rough-legged Hawks are from limited observational data (Craighead and Craighead 1956, Sylvén 1978). Knowledge of winter range fidelity is based on one hawk sighted over four successive winters (Sylvén 1978). In this paper I describe patterns of range use and range fidelity exhibited by Rough-legged Hawks during a study of this species' winter ecology in southeastern Idaho.

Research was conducted in 1982 to 1983 on the 2,315 km² Idaho National Engineering Laboratory (INEL). Big

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