

Chick Recognition in American Avocets: A Chick-exchange Study

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Chick recognition is central to an understanding of why adoption occurs in birds. If adults discriminate between their own and alien chicks, the chance of a chick being adopted decreases (Pierotti 1988). In contrast, lack of recognition may result in a high frequency of adoption. Several hypotheses concerning adoption make predictions about chick recognition. The nonadaptive "side-effect" hypothesis suggests that adults do not recognize their own offspring (Eadie et al. 1988, Choudhury et al. 1993). Adults should recognize their own offspring and those of related adults if adoption is based on kin selection (Holley 1984). If adults are reciprocal altruists, i.e. they adopt chicks of adults that might provide a similar service (Trivers 1971), they should recognize their young and the offspring of other altruists. The "intergenerational conflict" hypothesis (Pierotti and Murphy 1987) predicts that adults should recognize their young and reject unrelated young in order to direct parental care to their own offspring.

The potential for adoption depends on the age at which chicks can be recognized by their parents. The onset of recognition usually is synchronized with the onset of brood mobility, as in semiprecocial gulls (Graves and Whiten 1980), or at fledging, as in altricial passerines (Burt 1977, Balda and Balda 1978, Beecher et al. 1981). The timing of chick recognition also is important from a conservation viewpoint because it gives information on the potential for artificial adoptions or intraspecific cross-fostering of chicks in threatened or endangered species. To our knowledge, chick recognition has not been studied experimentally in precocial shorebirds.

American Avocet (*Recurvirostra americana*) chicks are precocial. Soon after chicks hatch, adults move their broods from the nest to feeding territories (Lengyel 1995). Adoptions frequently take place during brood movements at our study site. In 1993 and 1994, respectively, 19.8% ($n = 106$) and 32.2% ($n = 115$) of broods contained at least one adopted chick. Because chick recognition is crucial to an understanding of how and why adoption occurs, we conducted a chick-exchange experiment to reveal whether chick

recognition exists in American Avocets, and if so, to estimate its timing during chick development.

Methods.—Field experiments were conducted at Jay Dow, Sr. Wetlands (40°10'N, 120°20'W) in Lassen County, California, in 1993 and 1994. Details of the study site and general field methods are available in Robinson and Oring (1997). All chicks used in exchange trials were individually color-banded. Twenty adults (38.5% of total population of 26 pairs) were color-banded, with one or both adults marked at 12 nests. We followed brood movements on a daily basis.

Based on observations of aggression by adults toward older chicks in 1993, and pilot trials in early 1994, we divided experimental chicks into two age groups: ≤ 7 days old ("young" group) and ≥ 8 days old ("old" group). In fostering trials, chicks were transplanted to a different brood (referred to as "resident" chicks), whereas control chicks were reintroduced to their own family. We used same-aged chicks in fostering trials to eliminate the confounding effect of body-size differences between the experimental and the resident chicks. Thus, our 2×2 factorial experiment design had two levels of age (young and old) and two levels of treatment (foster and control).

Chicks and families were used in only one trial. Experimental broods and chicks were chosen at random. We determined the age group and selected the experimental chick first, and the treatment (control vs. fostered) second. If a fostering trial was selected, we randomly chose a foster family. Chicks were captured by hand, transported to the location of the foster family, and exchanged with a chick from the foster family (replaced chicks were kept at the observation point). After a 10-min acclimation period, we used instantaneous sampling every 15 s for 15 min to record the behavior of the adult closest to the foster chick. Because aggressive behavior was brief in pilot trials (duration of "alarming" behavior, $\bar{x} = 7.3 \pm \text{SD of } 2.65 \text{ s}$, $n = 6$; chasing, $\bar{x} = 1.8 \pm 0.40 \text{ s}$, $n = 3$), we believe that 15-s periods were enough to ensure independence between sequential observations. We also estimated distance between the closest adult and the chick.

In controls, the experimental chick was returned to its own family after a 15-min period, and the same sampling method was used after the 10-min accli-

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mation period. After trials, both experimental and replaced chicks were returned to their natal families.

Chick behavior was monitored during the 10-min acclimation period. Three chick behavior patterns were observed: (1) the chick quickly ran away from the foster family, (2) the chick remained crouched in one place, and (3) the chick stayed with and/or followed the family. In the first two cases, no interactions occurred between the foster parent and the experimental chick, whereas interactions occurred between them in the third case. In the latter case, foster chicks usually began feeding with the resident chicks and reacted to the adults' calls. Based on these observations, we decided *a priori* to conduct a trial only if some form of interaction occurred between the parent and the foster chick during the acclimation period, i.e. the chick acted as part of the foster family.

We divided adult behavior (defined after Hamilton 1975) into three groups: (1) acceptance (brooding, calling, leading, protecting, vigilance), (2) indifference (feeding, flying, preening, walking), and (3) aggression ("alarming," chasing). If adults behaved aggressively toward the experimental chick, the chick was considered rejected. Otherwise, the chick was considered accepted.

Six control and seven fostering trials were completed in both age groups (26 trials total). The mean age of young chicks was $4.5 \pm \text{SD of } 1.87$ days in controls (range 2 to 7 days), and 4.7 ± 1.80 days (range 2 to 7) in the fostered group ($t = -0.21$, $\text{df} = 11$, $P = 0.837$). The mean age of old chicks was 12.0 ± 3.23 days (range 8 to 16) in controls and 11.7 ± 3.04 days (range 8 to 17) in the fostered group ($t = 0.41$, $\text{df} = 11$, $P = 0.689$).

In statistical analyses, parametric methods were used when the assumptions of these tests were met. We used nonparametric tests for analyzing frequencies of individual behavior patterns because of the small sample size and the high frequency of "zero" values in the data.

Results.—The frequency of acceptance behavior decreased slightly with age (from 84.3% to 83.7% in controls, and from 76.0% to 75.3% in fostering trials for young and old chicks, respectively), but this effect was not significant (two-way ANOVA, $F = 0.13$, $\text{df} = 1$ and 22, $P = 0.719$). Adults exhibited acceptance behavior $84.0 \pm \text{SE of } 1.54\%$ (mean combined between age groups) of the time in control trials, and $75.7 \pm 1.67\%$ in fostering trials. The effect of treatment (control vs. fostered) was significant ($F = 13.34$, $\text{df} = 1$ and 22, $P < 0.005$), and the means were different in both age classes (Tukey HSD test, $q = 8.29$, $\text{df} = 1$ and 22, $P = 0.013$). Adults tended to call to their chicks more often than to alien chicks (Table 1). Frequencies of other acceptance behaviors also tended to be higher in controls than in foster trials, but the differences were not statistically significant (Table 1).

The frequency of indifferent behavior ($\bar{x} = 15.7 \pm$

TABLE 1. Frequency of acceptance behaviors by adult American Avocets toward control ($n = 12$) and fostered chicks ($n = 14$) (age groups combined). Data are percentages ($\bar{x} \pm \text{SD}$).

Behavior	Control	Fostered	H^a	P^b
Vigilance	66.8 ± 18.52	65.1 ± 16.89	0.32	0.816
Calling	9.0 ± 5.53	5.1 ± 9.10	5.87	0.059
Leading	5.2 ± 7.65	1.6 ± 4.37	2.58	0.367
Protecting	0.9 ± 1.63	1.8 ± 3.55	0.25	0.816
Brooding	2.2 ± 6.61	0.0 ± 0.00	—	—

^a Kruskal-Wallis test.

^b Significance levels adjusted for experimentwise error using the sequential Bonferroni method.

1.49% in controls and $19.6 \pm 1.38\%$ in fostering trials) did not differ between treatments (two-way ANOVA, $F = 2.06$, $\text{df} = 3$ and 22, $P = 0.135$). The effect of treatment was marginally significant ($F = 3.70$, $\text{df} = 1$ and 22, $P = 0.067$) and that of chick age was not ($F = 1.74$, $\text{df} = 1$ and 22, $P = 0.200$). Each indifferent behavior was equally likely in the control and fostered groups (Kruskal-Wallis tests, $P > 0.17$ for each behavior).

Adults did not show aggressive behavior to their own chicks. However, 6.9% of the behaviors recorded in fostering experiments were aggressive. Aggression usually started with alarm-calling by the adults toward the foster chick. Later, adults pecked at the chick, which was observed in each trial where aggression occurred. However, pecking was recorded in the behavioral sample only twice, because this behavior (which lasts for < 1 s) often took place outside instantaneous samples. Chicks usually crouched and froze when pecked at but did not leave the foster brood. In only one case did aggression result in the separation of a chick from the foster family.

Aggression was recorded in 5 of 14 fostering trials (chick ages 3, 9, 10, 12, and 17 days). Aggression also was observed outside instantaneous sampling times but within the experimental period in two fostering trials (chick ages 8 and 11 days). Therefore, we classified these as rejections even if no aggression was recorded in the behavioral sample. In six of seven rejections, aggression first occurred in the first 5 min of the trials, and in one case it occurred after 7 min. The mean time period elapsed until the first aggression ($3.3 \pm \text{SD of } 2.06$ min) was significantly shorter than that expected from a uniform distribution of aggression during the 15-min period (expected time from random model based on uniform distribution, 7.5 ± 1.41 min; Mann-Whitney test, $U = 46.50$, $P = 0.005$). Within the foster group, aggression was directed more often toward old chicks (82.9%, $n = 35$ observations) than toward young chicks (17.1%; $G = 15.95$, $\text{df} = 1$, $P < 0.001$). Of 14 fostering trials, six young chicks were accepted and one rejected, whereas only one old (13 days old) foster chick was ac-

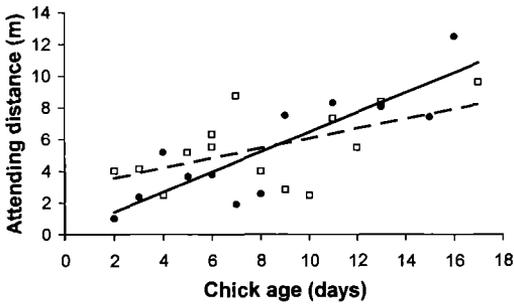


FIG. 1. Attending distance as a function of chick age in American Avocets. Linear regression; control trials (solid dots, solid line): $r^2 = 0.728$, $df = 10$, $P < 0.001$; fostering trials (open squares, dashed line): $r^2 = 0.314$, $df = 12$, $P = 0.037$.

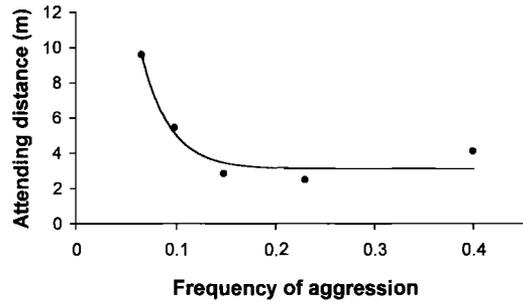


FIG. 2. Attending distance as a function of frequency of aggression in American Avocets. Frequency of aggression is given as the number of aggressive behaviors per total number of observations in a 15-min sample. Nonlinear regression; $r^2 = 0.941$, $df = 3$, $P < 0.01$.

cepted and six rejected (conditional binomial exact test [Rice 1988], two-tailed $P = 0.011$).

Adults attended older chicks at a greater distance in both control and fostered groups (Fig. 1). The slopes of the regression lines were marginally different (ANCOVA, interaction $F = 3.05$, $df = 1$ and 22 , $P = 0.095$). Attending distance was smaller when chicks were rejected than when they were accepted (ANCOVA with chick age as covariate, $F = 5.33$, $df = 1$ and 11 , $P = 0.041$). This suggests that aggression was related to attending distance, which also is supported by a negative relationship between attending distance and frequency of aggression (Fig. 2).

Discussion.—Our experiment provided three results. First, adult avocets appeared to recognize their chicks because acceptance behavior was more frequent in control trials than in fostering trials. Adults showed no aggression toward their own young. Aggressive behavior was directed toward alien chicks, and although aggressive periods made up only about 7% of trials (i.e. 1.05 min in each 15-min trial), aggression by adults was severe (e.g. pecking) during these periods.

Second, the higher frequency of aggression toward old fostered chicks suggests that parents discriminate against alien chicks after the first week post-hatching. However, the fact that acceptance behavior was more likely to occur in controls than in fostering trials, regardless of chick age, indicates that some discrimination may exist during the first week of the chicks' life. Therefore, it is possible that chick recognition is present at earlier ages and becomes elaborated later, as chicks develop. Our only observation of aggression toward a young (3-day-old) chick is equivocal, because adults showed aggression to the chick while being involved in a territorial fight with a neighboring pair. Despite the fact that we used chicks of different ages (2 to 17 days) in the trials, our randomization procedure, and the finding that aggression was more frequent at ages older than 7 days,

suggest that chick recognition can be detected after the first week posthatching in the American Avocet.

Third, attending distance increased with chick age, probably resulting from the older chicks' higher mobility and better antipredator abilities. Adults attended chicks that they rejected at a closer distance than those that they accepted, which may indicate increased alertness and intolerance toward alien chicks by adults. Moreover, because attending distance decreased with frequency of aggression, attending distance may be an indicator of aggression.

Chick-recognition studies in gulls and terns have interpreted aggression as rejection of the alien chick, and lack of aggression as acceptance of the chick (Davies and Carrick 1962, Buckley and Buckley 1972, Miller and Emlen 1975). However, this approach has been criticized because aggression results from intolerance toward strange chicks (Shugart 1977). Choice trials, on the other hand, test an adult's acceptance behavior directly. These tests generally require: (1) local attachment of a brood, and (2) a specific aspect of parental care on which the choice is based, e.g. feeding the chick. Because precocial species lack these characteristics, the chick-exchange method appears to be the only available option to apply in such species.

Chick behavior has been reported to influence aggression by adults in some species of semiprecocial gulls (Miller and Emlen 1975) and has been believed to be the basis of parental recognition in others (Knudsen and Evans 1986). In gulls, aggression by adults usually occurred if the chick behaved "unnaturally," e.g. crouched or attempted to return to its own parents. To eliminate the effect of such unnatural chick behavior, we conducted trials only if the experimental chick had been observed integrated in the foster brood, i.e. the chick followed the family. Empirical observations suggest that chicks behaved similarly when introduced to familiar (control trials)

and unfamiliar (foster trials) conditions, because in both situations they spent most of their time feeding. Foster chicks usually began feeding at the same time when the resident chicks did. Moreover, foster chicks, except for one case, stayed with the foster brood for the duration of trials even if adults showed aggression toward them. These findings suggest that there was no motivation on the part of chicks to return to their own parents, and that chicks behaved similarly towards familiar and unfamiliar adults.

The fact that adults accepted six young foster chicks and only one old chick may result from: (1) differences in behavior of chicks of different ages, and (2) the ability of adults to discriminate older chicks. However, lack of aggression toward old chicks in the control group suggests that the discrimination process of adults is not based solely on age-specific differences in behavior.

Our results may be biased if rejection takes longer than 15 min in avocets. However, the fact that aggression was more likely to occur early in trials suggests that the 15-min experiments were long enough to detect differences in behavior.

The timing of aggressive chick recognition in avocets appears counter to that in gulls and terns, where chick recognition develops just before the onset of brood mobility (Davies and Carrick 1962, Buckley and Buckley 1972, Miller and Emlen 1975). Avocet chicks are mobile and may be adopted into alien broods within a few hours after hatching, indicating that the degree of recognition that could prevent adoptions develops after the onset of mobility. Such delayed recognition also has been reported in altricial species, e.g. swallows (Burt 1977). The delay in avocets may result either from precociality, i.e. the cost of tolerating an alien chick in the brood is probably low, or from the high risk of rejecting one's own chick (Knudsen and Evans 1986).

In summary, our results suggest that avocets recognize their own young. It is possible that chick recognition exists in a less well-developed form in early stages of chick development and is more strongly developed as chicks become older. This process makes it likely that early adoption has little cost in precocial shorebirds so that selection for chick recognition is absent (neutral hypothesis). Alternatively, adoption might provide reproductive benefits by increasing the likelihood that a parent's own chicks survive (e.g. via a dilution effect), which may be more important in young broods if the risk of predation is higher than for older broods. Additional studies of brood success are needed to evaluate these potential explanations.

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Implications of Frequent Habitat Switches in Foraging Bar-tailed Godwits

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Temporal variation in avian foraging behavior spans a range of scales, from annual (Hejl and Verner 1990, Petit et al. 1990, Szaro et al. 1990), between-season (Ford et al. 1990, Lundquist and Manuwal 1990), and within-season (Hejl and Verner 1990, Miles 1990, Sakai and Noon 1990) to a matter of a few hours (Holmes et al. 1978). Among nonbreeding shorebirds, temporal variation in foraging behavior frequently manifests itself via habitat selection (Myers 1984). Switches between foraging habitats by shorebirds may involve movements between littoral and upland sites (Goss-Custard 1969, Prater 1972, Page et al. 1979) or between littoral habitats (Connors et al. 1981). Most of the foraging-habitat switches documented for nonbreeding shorebirds are linked to changes in habitat availability and foraging profitability across a tidal cycle (Connors et al. 1981, Myers 1984). In this paper, I present data on a population of staging shorebirds that exhibited repeated, alternating habitat shifts within single tidal cycles.

Bar-tailed Godwits (*Limosa lapponica baueri*) stage each fall along the Bering Sea coast of southwestern Alaska (Gabrielson and Lincoln 1959, Gill and Handel 1981, 1990). I studied foraging godwits that switched between an intertidal flat and upland dwarf shrub tundra. My objective was to document the temporal pattern of habitat switching to determine if it was consistent with the tidally induced switching reported for shorebirds elsewhere.

Study area and methods.—I studied juvenile godwits

at Duchikthluk Bay on the south side of Nunivak Island, Alaska (59°49'N, 166°09'W). Duchikthluk Bay is a 32-km² shallow lagoon fed by the Duchikmiut River and five unnamed streams, and open to the Bering Sea through a 450-m wide channel. Duchikthluk Bay is bordered on the east and west by tidally influenced graminoid meadows, and on the north and south by low uplands covered with sedge, lichen-sedge, and dwarf shrub meadows.

Several assistants and I observed godwits along the south shore of Duchikthluk Bay near Kingaktamiut, a Yup'ik Eskimo summer fishing camp. We used a permanent fish camp tent frame for observations of both intertidal and upland foraging habitats. Several dozen godwits foraged on a 117-ha intertidal sand and mudflat 100 m northwest of the observation site, and on a 0.1-ha patch of dwarf shrub tundra immediately south of the observation site that was rich in crowberries (*Empetrum nigrum*).

Godwits were observed on the berry patch during receding tides by one to four observers on 11 days between 7 and 30 September 1991. The proximity of the observers to the birds (<50 m), the low stature of the vegetation (<3 cm), and the distinctive foraging behavior of fruit-eating godwits facilitated quantitative observations. As godwits arrived on the patch, each observer selected a focal individual. To avoid double-sampling the same individual during a given foraging bout, observers selected focal individuals on opposite sides of the flock. Individuals were not randomly selected, however, nor were foraging bouts independent (i.e. the same individual might have been sampled during different visits to the patch).

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