

MATE FEEDING BY WESTERN AND CLARK'S GREBES¹

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Abstract. Of the grebes that have been studied, Western Grebes (*Aechmophorus occidentalis*) and Clark's Grebes (*A. clarkii*) are unique in having a short period of intensive mate-feeding behavior that immediately precedes nest building and egg laying. The evolution of mate feeding in these two fish-eating grebes may be the result of social selective pressures relating to mate and nest-platform guarding.

Key words: Mate feeding; courtship feeding; Western Grebe; Clark's Grebe; Aechmophorus.

INTRODUCTION

Males of many bird species provide food for their mate (Lack 1940, Smith 1980). Traditionally, such provisioning was thought to serve only a symbolic function in strengthening the pair bond (Lack 1940, Andrews 1961), but recent studies suggest that in many species it may provide an important source of female nutrition during egg production (Royama 1966, Nisbet 1977, Tasker and Mills 1981, but also see Poole 1985). If pair formation in birds is acknowledged as a continuous, multi-step process of mate assessment (Hunt 1980, Nuechterlein and Storer 1982, Halliday 1983), mate feeding in many species may function as the final, precopulatory step in mate choice.

Both the timing of mate feeding and the types and quantity of food offered by males varies widely among species. In some groups, such as corvids (Goodwin 1976) and accipiters (Cramp and Simmons 1980), the male provides nearly all of the food for the female throughout incubation. In other species, including most grebes (family Podicipedidae), the only known records are of small tidbits being offered. Until recently, most such observations have been lumped together and described simply as courtship feeding (Smith 1980). In this paper, we use the term mate feeding rather than courtship feeding if the behavior appears to be directed solely towards feeding the individual's mate and is not associated with earlier ritualized courtship activity.

Except for Nero's (in Palmer 1962) brief mention of "courtship" feeding in Western Grebes (*Aechmophorus occidentalis*), there are very few documented cases of regular mate-feeding behavior in any of the 21 grebe species. In most of these cases, published examples appear to be only of occasional offerings of small bits of food or feathers to a mate, often during exchange of incubation duties (Ulfstrand 1964; Bandorf 1970; Fjeldså 1973, 1985; Cramp and Simmons 1977). In some other cases it is unclear whether the food morsel actually was being offered to the mate or was passed to a mate for subsequent consumption by the young.

Western Grebes and Clark's Grebes (*A. clarkii*), however, appear to be exceptions. In both species mate feeding is common, involves large quantities of food, and occurs regularly between mated pairs prior to nest initiation. In this paper, we describe this behavior and examine its behavioral, seasonal, and functional contexts.

METHOD

Observations on mate feeding were made as part of studies of the behavior of Western and Clark's grebes (Nuechterlein 1981a, 1981b; Nuechterlein and Storer 1982) conducted between 1963-1987. Both species are colonial and, in areas where their ranges overlap, they frequently nest in mixed-species colonies. This allowed us to observe mate feeding by both species simultaneously, although Western Grebes were more common in all of the study populations. Colony sizes varied widely, from 20 to several thousand individuals, and mean nearest neighbor distances for nests averaged between 2 and 4 m (Nuechterlein

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1975). Incubation stages of eggs were determined by egg-flotation techniques (Westerkov 1950), as modified for Western Grebes by Nuechterlein (1975).

Primary study areas included the Delta Marsh, Lake Manitoba, Canada, the Bear River Marsh, Utah, and the Klamath Basin National Wildlife Refuges near the Oregon-California border. Observations were made using binoculars and a 15–60× spotting scope. Relative lengths of fishes being fed were estimated by comparisons with the size of the male's bill. We also filmed and tape-recorded the behavior using Bolex and Beaulieu 16-mm movie cameras and a Uher Report-L tape recorder equipped with a Dan Gibson parabolic microphone. Sound spectrograms were made using a Uniscan II real-time digital analyzer. Display terminology is from Nuechterlein and Storer (1982).

RESULTS

SEASONAL AND BEHAVIORAL CONTEXTS

In total, we have observed at least 40 bouts of mate feeding by Clark's Grebe pairs and over 230 by Western Grebes. Although these pairs were unmarked, mate feeding was observed regularly on all of the study areas and probably is characteristic of most, if not all pairs. Most mate feedings occurred between 1 May and 15 June, prior to the initiation of nesting in most colonies.

Mate-feeding pairs rarely participate in the vigorous courtship displays of the Rushing Ceremony (Nuechterlein and Storer 1982), which are performed by unpaired birds during the same time period. Thus, although mate feeding occurs regularly in pairs in the later stages of pair formation, it is not performed as part of the early, elaborate courtship ceremonies. Instead it occurs during the 1–3 week pair-liaison period that occurs between the time that two pair members first remain together and the time that they begin to build the nest platform, upon which copulation usually takes place.

During this period, pair liaisons are conspicuous and mates usually remain close together. Foraging dives are often synchronous, and partners regain eye contact after each dive. If separated for longer than 1–2 min, either or both birds may give Advertising calls. These are recognized individually by the birds (Nuechterlein 1981a), and provide a means of maintaining contact in an often-crowded colonial setting. If the

separation has been greater than a 2- to 3-min period the pair may perform a brief Greeting Ceremony when they rejoin (Nuechterlein and Storer 1982).

BEHAVIORAL DESCRIPTION

We observed no obvious differences in the mate-feeding behavior of Western and Clark's grebes. At all study area locations, mate feeding was observed repeatedly in feeding areas, especially near bridges, culverts, and dams, where the running water evidently attracted fish.

Mate-feeding bouts usually lasted 1–2 hr. Often a pair remained in a fairly well-circumscribed area, which both birds defended from intruders while feeding. When a pair first arrived in the morning, usually both the male and the female dived simultaneously for food. After several dives, the female began to demand food by repeatedly giving loud begging calls between dives of the male until he began feeding her. In the final stages of a mate-feeding bout, the female often placed one leg under the wing ("leg shipping," Storer 1969) and stopped diving altogether.

For long periods, especially when the water was turbid and fishing success poor, the male foraged while the female remained on the surface. While the male was submerged, the female ceased begging, but as soon as the male surfaced from a foraging dive, she again started begging, placing her head down and somewhat forward, crest flattened against her head and bill opened (Fig. 1A), as she gave the characteristic begging call. This call is a repeated double note, rather harsh and guttural (Fig. 2A–D). It might be rendered *tuk-a, tuk-a, tuk-a*, although neither of these syllables captures its guttural quality. When the male was successful, the female begged until he fed her. If the male surfaced from an unsuccessful foraging dive, the female usually begged constantly until he dived again. Once a male brought a fish to the surface, we never saw him refuse to feed it to his mate, although sometimes a resting male refused to dive in response to the weak begging calls of a nearly-satiated female.

The intensity of begging became stronger when a male surfaced with a fish in his bill and still stronger if the male did not feed the female immediately, either because they were some distance apart or because he took time to pinch and reposition repeatedly a catfish or other spiny fish in his bill. At these times, the female swam with

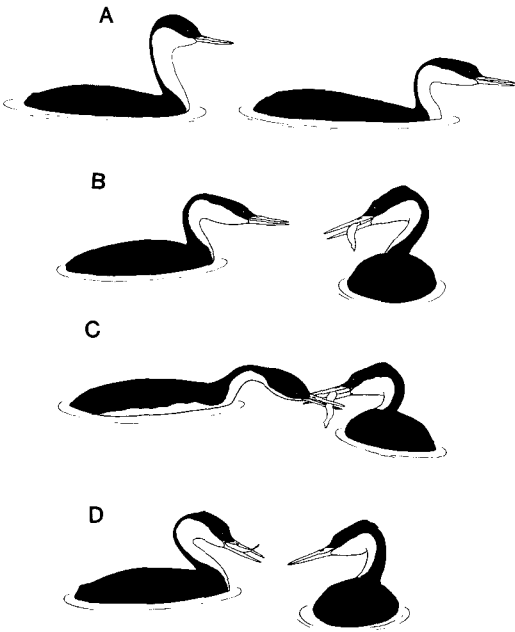


FIGURE 1. Mate feeding by a male Western Grebe drawn from cine film. (A) Normal swimming posture (left) and begging posture (right) of female; (B–D) male feeds fish to female. Bouts of mate feeding commonly last 1–2 hr or until the female is satiated.

her body very low in the water, her neck awash, her head pointed somewhat upward, and her bill opened wider than in low-intensity begging. Females were occasionally observed to beg from males who appeared to be mated to other females, but in all such instances the males passed by these females and proceeded to feed their own mates. Female begging calls are individually distinct (Fig. 2A–D), and males probably recognize their mates by these vocal differences.

TIMING OF MATE-FEEDING BEHAVIOR

Mate feeding appears to peak shortly before egg laying. This was best documented for the Channel colony on the Delta Marsh, Manitoba, in 1974. At this small colony (30 nests), both mate feeding and nesting-colony formation could be monitored simultaneously, because both occurred along a small channel isolated from other colonies.

Mate feeding by birds of the colony was first observed at the channel on 31 May, and peaked on 2–3 June when 15–20 different males were observed feeding their mates in mid-morning ob-

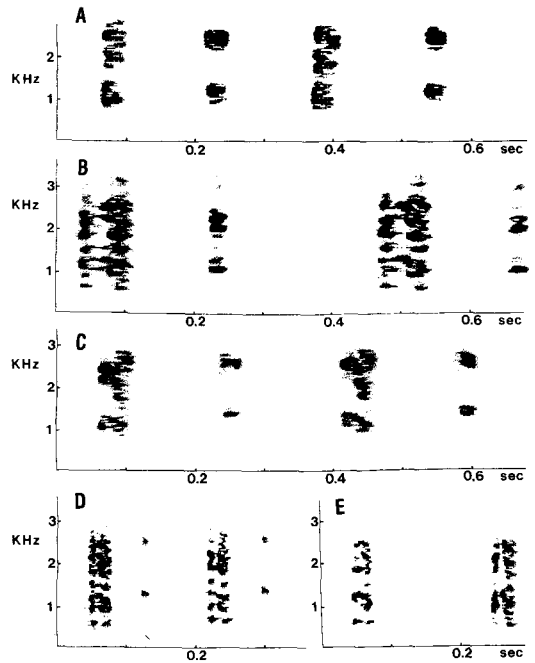


FIGURE 2. Individual differences in the begging calls of four different Western Grebe females (A–D) given during mate feeding. Begging calls consist of repeated *tuk-a* notes given in long bouts. Aggressive calls (E) given by the same female as D above were very similar in structure to the *tuk* portion of the begging call.

servation periods. Clutch initiation in this colony peaked 4 days later, when 11 of the 29 clutches were initiated (Fig. 3). Nest building by Western Grebes usually begins 1–2 days prior to clutch initiation, so we estimate that the peak in nest-building activity at the colony occurred on 4–5 June, immediately following the peak in mate-feeding activity at the channel. By 13 June all nests had been initiated. Mate feeding ceased abruptly once a pair began nest building, and after that date mate-feeding activity at the channel also ceased.

QUANTITY OF FOOD

The actual amount of food that a male feeds its mate during a bout of mate feeding is difficult to determine, but appears to be considerable. In many cases, length of feeding bouts appeared to be determined by female satiation. Toward the end of feeding bouts, females often stopped begging and refused fish that were offered, particularly if they were large ones. Once several such refusals took place, the male would either stop

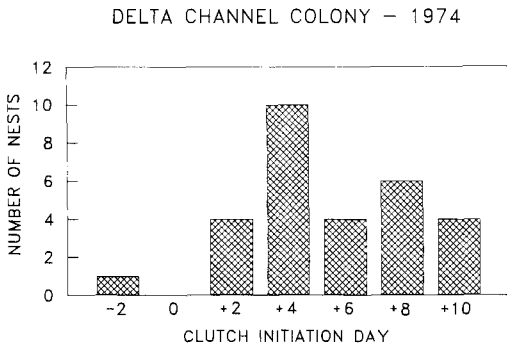


FIGURE 3. Initiation of clutches in relation to mate-feeding activity at the Delta Channel colony. The number of clutches initiated in each 2-day period is plotted relative to the peak in mate-feeding activity (Day 0), which occurred on 2-3 June (see text).

diving altogether or continue diving but not bring any further fish to the surface for the female.

We have data for an entire bout of mate feeding for one of the male Western Grebes at the Channel Colony. This individual was easily identified by his unusual bill markings, and his mate remained in sight on the surface during the entire feeding bout. In 1 hr this male fed his mate nine large (7-10 cm) spot-tailed shiners (*Notropis hudsonius*), with a conservatively estimated total wet weight of at least 90 g. At the end of the bout the female refused further offerings.

DISCUSSION

Our observations of mate feeding in Western and Clark's grebes support Smith's (1980) interpretation of courtship feeding as demand behavior by females. The calls of a begging female are often insistent, particularly when a male delays in diving or giving up a fish. Both calls and posture appear to be nearly identical to those of older chicks begging food from their parents.

High-intensity begging calls also closely resemble the calls that both members of a pair give when threatening intruders. In one instance we were able to obtain recordings of a female as she first begged from her male (Fig. 2D), then immediately threatened a neighboring bird (Fig. 2E). Sound spectrograms of this transition to an aggressive call showed that it had nearly identical structure to the *tuk* portion of the begging call. Aggressive calls, however, are given with the crest raised rather than flattened and are characteristic of both sexes.

Our studies suggest that mate feeding occurs

regularly in Western and Clark's grebes, and that it may provide females with an important source of energy for egg formation. During mate feeding the male always feeds the begging female, never the reverse. Although occasionally the fish is passed back and forth, this is rare and appears to be associated with female satiation or with fish that are difficult to swallow, such as spiny catfish or very large fish.

This unilateral feeding of females by males contrasts sharply with all of the early pair-formation displays (Nuechterlein and Storer 1982), in which the roles of the male and the female are similar or identical. Also, mate feeding does not occur in regular association with any of these early courtship display sequences, but instead takes place subsequent to the formation of pair liaisons. For Western and Clark's grebes, we therefore avoid using the term courtship feeding to describe this behavior, because this term suggests a ritualized function.

Since mate feeding in a pair may continue for a week or more, this behavior potentially provides a significant direct energy contribution by males to egg formation. This view is supported by the close association of mate feeding with egg laying and by the large quantities of fish that are fed. Mate feeding strongly resembles parental feeding of chicks and usually appears to continue until the female becomes satiated.

For Western and Clark's grebes, an average clutch of three to five eggs weighs between 120 and 200 g, or up to 20% of the female's body weight. Since pairs of most grebe species share incubation duties (Cramp and Simmons 1977), the period during which the eggs are developing is the only obvious one in which the female's energy requirements are considerably greater than those of the male. Mate feeding by male Western and Clark's grebes during this short period may allow females to acquire large quantities of food with little energy expenditure of their own. Once incubation begins, the males share in it and females are able to feed. Mate feeding in both grebe species then ceases abruptly. This is in contrast to many species, such as corvids and accipiters, that have female-only incubation and continue mate feeding throughout incubation.

Why mate feeding in grebes occurs only in the genus *Aechmophorus* remains conjectural. Clark's and Western grebes, the only two members of the genus, are strongly colonial fish-eaters. Within this context, several important selective fac-

tors acting in consort on both males and females may be involved: (1) Nests are close together and need constant guarding. During colony formation, partially built nest platforms that are left unguarded are rapidly taken over by other pairs seeking nest sites. Egg dumping in unguarded nests is also frequent in colonial grebes. If nest platforms are not defended constantly during the entire egg-laying period, they may be immediately usurped or parasitized by other pairs. (2) For the fish-eating grebes, very little food is usually available at the colony site itself. Instead, primary foraging areas may be located a kilometer or more from the colony. (3) Guarding of the mate may preclude separation of a pair for feeding during the nest-building and early egg-laying periods, when most copulations occur. Unlike waterfowl, grebes lack an intromittent organ, and copulations by a pair do not occur on open water prior to building a nest platform (McAllister and Storer 1963).

Taken together, these three factors may necessitate a short period of fasting or energy deficit for the fish-eating colonial grebes that occurs just prior to egg laying. If both members of the pair stay at the colony, neither is able to fish, while if both leave to feed, the nest platform will be lost. To finish laying a large clutch, females therefore must carry sufficient energy reserves, and this would provide strong selective pressure on males to supplement their mate's reserves prior to nest establishment. Once the fertile laying period has passed, pair members need not remain together at the nest site, since one bird incubating on the platform is sufficient to dissuade most nest-usurpers.

This argument is somewhat similar to that of Hunt (1980) who suggested that courtship feeding in many seabirds may be an adaptation that allows females to obtain the extra energy needed for the production of eggs without having to leave the nest for long periods to forage once their initial eggs have been laid. We agree with Poole (1985), however, that mate feeding also may directly aid males in ensuring mate fidelity and confidence of paternity.

Since only a single food item can be delivered per trip in all grebe species, relative size of individual food items also becomes important in determining the relative costs and benefits to males that attempt to feed their mates. Other things equal, selection pressures favoring mate feeding in the fish-eating grebes should be par-

ticularly strong, since fish are large food items that males can carry efficiently in their bills to females. In Common Terns (*Sterna hirundo*), males court unmated females by bringing individual food items in their bills, and Taylor (1979) found that such males chose fish that were relatively larger than those normally consumed.

This prey-size argument suggests that males of the highly colonial Eared Grebe (*Podiceps nigricollis*), for example, may find it unprofitable to provide females with food sufficient to satiate them because they feed primarily on small invertebrates. If regular mate feeding does occur in other grebes, we therefore suspect that it is most likely to be found in other colonial fish-specialists, such as the little-studied, flightless Taczanowski's Grebe (*P. taczanowskii*) of Lake Junin, Peru.

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