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# Brood Parasitism and Communal Egg Dumping in the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*)

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***Abstract*.—Conspecific brood parasitism occurs in many species of birds, especially colonially breeding species with precocial offspring. During 2010–2019 we monitored nesting colonies of the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*Aechmophorus clarkii*) at Clear Lake, California. Maximum mean clutch size in three large colonies ranged from 2.29–3.12 eggs/nest (range, 1–14). Brood parasitism in 33 marked nests with 1–4 eggs occurred at a rate of 0.04–0.17 egg/nest/d and in 2.6–10.4% of nests/d. Nests with up to 10 eggs were usually incubated in well-maintained nests. We encountered 51 nests with unusually large clutches of 11–31 eggs, presumably laid by multiple females, representing 0.16% of all nests encountered. All were disintegrating nests unattended by grebes, except for one well-maintained nest with 18 eggs incubated by a mixed pair of grebes. Brood parasitism in three of these nests occurred at a rate of 0.0–4.0 eggs/nest/d. Such communal egg dumps occurred only in larger colonies with a minimum of 134 nests. The number of nests and number of communal egg dumps in a colony were positively correlated. Conspecific and interspecific brood parasitism by females of the two species is more extensive than previously realized and appears to be a common and potentially adaptive reproductive strategy.**

*Key Words*.—breeding; California; Clear Lake; clutch size; coloniality; nesting; Podicipedidae; reproduction.

## Introduction

In birds, conspecific or intraspecific brood parasitism results from females laying eggs in the nests of conspecifics without subsequently incubating the eggs or caring for hatchlings (Yom-Tov 1980). It occurs across a wide taxonomic spectrum, including at least 256 species of 44 genera (Yom-Tov 2001; Yom-Tov and Geffen 2017), and is especially likely to occur among colonially breeding species with precocial offspring because they tend to lay larger clutches than species with altricial offspring, initiation of incubation is often delayed until most or all of the eggs are laid (which may leave the nest unguarded for several days), and the costs of raising parasitic offspring are lower than for species with altricial offspring that require more time to develop (Petrie and Møller 1991; Sorenson 1992; Johnsgard 1997; Yom-Tov 2001; Yom-Tov and Geffen 2017). Some species engage in an extreme form of conspecific brood parasitism, referred to as dump nesting (Mackie and Buechner 1963), pre-hatch brood amalgamation (Eadie et al. 1988), or egg dumping (Yom-Tov 1980), in which multiple females lay large numbers of eggs in a single unattended nest.

Many species of grebes (Podicipedidae) breed colonially and all have precocial offspring (Fjeldså 2004). Conspecific brood parasitism has been reported in at least six of the 23 species of grebes (Yom-Tov 2001): the Red-necked Grebe (*Podiceps grisegena*), Great Crested Grebe (*P. cristatus*), Eared Grebe (*P. nigricollis*), Silvery Grebe (*P. occipitalis*), Western Grebe (*Aechmophorus occidentalis*), and Clark's Grebe (*A. clarkii*). The Western Grebe and Clark's Grebe are large, morphologically similar, and occasionally hybridizing species of piscivorous birds that breed on floating nests in mixed-species colonies in lacustrine ecosystems in western North America (Storer and Nuechterlein 1992; http://birdsoftheworld.org/bow/species/wesgre; http://birdsoftheworld.org/bow/species/clagre). Up to six eggs are typically laid by a mated pair in a nest (Storer and Nuechterlein 1992; LaPorte et al. 2014, http://birdsoftheworld.org/bow/species/wesgre). Larger clutches and broods with mixed species may result from conspecific and interspecific brood parasitism (Storer and Nuechterlein 1992; LaPorte et al. 2014, http://birdsoftheworld.org/bow/species/wesgre). Nuechterlein (in Rohwer and Freeman 1989) reported brood parasitism in 1.8% of Western Grebe nests based on eggs added to incubated clutches. Finley (1907) was the first to report unusually large clutches of up to 16 eggs, that had never been incubated, in Oregon. Bent (1919) published a photograph of 11 eggs in a well-maintained nest in Saskatchewan and speculated that unusually large clutches were dumped indiscriminately by several birds, but never hatched. In this paper we provide new quantitative data on the occurrence of brood parasitism, including unusually large clutches of dumped eggs, and demonstrate that brood parasitism is much more extensive than previously realized in the Western Grebe and Clark's Grebe.

## Methods

***Study area*.—**Clear Lake (39°01'N, 122°46'W) is a large and relatively shallow lake, comprising an area of 180 km$^2$ with 114 km of shoreline and a maximum depth of 18 m, in Lake County, northern California, USA (Horne and Goldman 1972). The Western Grebe and Clark's Grebe nest together in colonies of up to 4,721 nests at Clear Lake, with most nests (84.9%) attended by Western Grebes (Hayes et al. 2022). The natural history and anthropogenic impairments of the lake are summarized by Suchanek et al. (2003) and Richerson et al. (2008).

***Sampling methods.***—We conducted surveys of nesting grebes at Clear Lake and adjacent wetlands during 186 d of field work between 8 April and 3 October of 2010–2019, with an average of 18.6 surveys per year (standard deviation = 7.2; range, 7–29 due to variable funding). The surveys were usually conducted from a canoe but some were conducted from a motorboat or from land. During each survey we counted the number of nests and occasionally the number of eggs on nests within each colony. A colony was defined as one or more nests separated by a gap of at least 400 m or by a minimum swimming distance of 400 m around land or dense aquatic vegetation from the nearest nest of an adjacent colony, even if only one nest was present at the site.

To determine the typical clutch size, we counted the number of eggs in each nest in the two largest colonies: Rodman Slough South on 6 and 13 August 2010 and at Anderson Marsh Southeast on 6 and 15 August 2010. We chose the date with the largest clutch size at each colony and combined the data to represent the typical clutch size of *Aechmophorus* grebes. Although we often noted clutch size of nests during subsequent years, we did not repeat large-scale egg counts to avoid excessive disturbance of nesting grebes until we encountered an unusually large number of eggs in a colony at Indian Island on 30 July 2019. We identified the parent incubating eggs on some nests, but due to the difficulty of determining the species for both individuals of each pair attending each nest, we combined the data for all nests for analysis.

Brood parasitism can be difficult to detect. The interval between laying the first egg and the last egg ranges from 3–6 d (Storer and Nuechterlein 1992; http://birdsoftheworld.org/bow/species/wesgre). To determine whether new eggs were laid on nests more than 1 week after eggs were present, which is more suggestive of brood parasitism than a mated pairing adding new eggs, we marked nests at the Rodman Slough South colony with numbered flags on stakes and counted the number of eggs on each nest on 13 August 2010. We subsequently returned to count the eggs on each numbered nest on 20, 27, and 31 August 2010. We did not repeat this method to avoid excessive disturbance of nesting grebes. We identified the parent incubating eggs on some nests, but due to the difficulty of determining the species for both individuals of each pair attending each nest, we combined the data for all nests for analysis.

Although we did not make an effort to observe eggs in all nests during the study period, nests with unusually large numbers of eggs were more conspicuous than nests with typical clutches because the eggs were seldom covered by an incubating grebe. Because we often observed grebes incubating on nests with up to 10 eggs and rarely observed grebes incubating on nests with more than 10 eggs, we defined communal egg dumps as nests with > 10 eggs. On all such nests, we counted the number of eggs and identified any accompanying adults. We estimated distances (nearest 1 m) between closely spaced communal egg dumps visually if close or measured with a laser range finder.

During 2014–2017, we monitored selected nests with up to six motion-activated cameras (Trophy Cam Bone Collector RTAP Night Vision and Trophy Cam HD Aggressor No Glow; Bushnell Outdoor Products, Overland Park, Kansas, USA). Each camera was bolted to a U-channel post pushed into the substrate and aimed at one or more active nests with variable numbers of eggs. We subsequently examined photographs for evidence of brood parasitism.

***Statistical analysis.***—We combined data for all 10 y for analysis. We used Spearman Rank Correlation Coefficient ($\alpha$ = 0.05; Zar 2010) to determine if the number of nests correlated to the number of egg dumps within colonies. All means are given ± 1 standard deviation.

## Results

During 2010–2019, we counted 31,234 grebe nests in 150 colonies at 37 sites along the shores of Clear Lake. The maximum mean clutch size in the two largest colonies in 2010 occurred on 6 August, with 2.29 ± 0.94 eggs/nest (range, 1–5; n = 76 of 334 nests) at Rodman Slough South and 2.37 ± 1.09 eggs / nest (range, 1–7; n = 294 of 440 nests) at Anderson Marsh Southeast. The vast majority of nests (97%) in these colonies combined had 1–4 eggs, with only 3.0% of nests containing > four eggs (Fig. 1). The maximum mean clutch size in the largest colony in 2019 occurred on 30 July, with 3.12 ± 2.42 eggs / nest (range, 1–14; n =132 of 1,516 nests) at Indian Island. Although most nests had 1–4 eggs, 15.2% had > four eggs (Fig. 1).

Eggs laid by brood parasites after a clutch of eggs were laid by a host were often distinguishable from the eggs of a host by being distinctly paler in color because the pale blue color of freshly laid eggs was gradually stained brown by wet nest vegetation (Fig 2). Parasitic eggs laid before the final egg of a host was laid, however, should overlap in age with the eggs of a host and be similar in color. One or more distinctly paler eggs often occurred among darker eggs in clutches with as few as two eggs, but because of subtle variation in egg coloration across a continuum from pale blue to brown, it was often difficult to distinguish between host and parasitic eggs, so we did not attempt to quantify egg coloration.

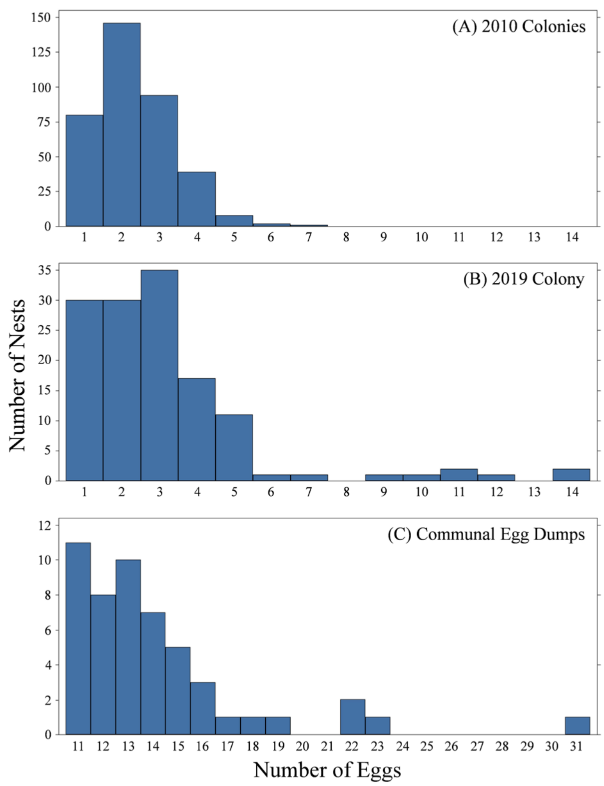


**Figure 1**. Examples of variation in clutch size (number of eggs in nest) of Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) nests at Clear Lake, California. (A) Rodman Slough South and Anderson Marsh Southeast colonies combined in 2010 (n = 370 nests). (B) Indian Island colony with six communal eggs dumps in 2019 (n = 132 nests). (C) Communal eggs dumps (> 10 eggs / nest) during 2010–2019 (n = 51 nests).

Of 102 marked nests with eggs (date of laying unknown) on 13 August 2010, 33 still had 1–4 eggs on both 20 and 27 August 2010. It was uncertain whether all of these eggs were being incubated. The number of eggs on 27 August (> 6 d after the first eggs were laid) decreased on 10 nests, remained the same on 16 nests, and increased by 1–3 eggs (mean = 1.7 new eggs/parasitized nest, n = 10 eggs) on six nests, including four nests with only one egg on 20 August. Thus, 10 eggs presumably laid by brood parasites were laid among 33 active nests during 7 d at a rate of 0.04 egg/nest/d, and 18.2% of nests were parasitized during 7 d at a rate of 2.6% of nests/d. Of 12 marked nests that still had eggs on both 27 and 31 August 2010, the number of eggs on 31 August decreased on four nests, remained the same on three nests, and increased by 1–2 eggs on five nests (mean = 1.7 new eggs/parasitized nest, n = 18 eggs), including two nests with only one egg on 27 August. Thus, eight eggs presumably laid by brood parasites were laid among 12 active nests during 4 d at a rate of 0.17 egg/nest/d, and 41.7% of nests were parasitized during 4 d at a rate of 10.4% of nests/d.

The grebes usually incubated and defended up to 10 eggs on well-maintained nests (Fig. 2); however, the grebes rarely incubated eggs on nests with > 10 eggs. During the study period we encountered 51 nests with 11–31 eggs in a nest (Figs. 1–2), representing at least 0.16% of all nests encountered. These communal egg dumps occurred in disintegrating nests unattended by grebes except for one well-maintained nest with 18 eggs (Fig. 2) incubated by a male Clark's Grebe and a female Western Grebe for at least 7 d (8–15 July 2016) in the Rodman Slough Northwest colony. Communal egg dumps occurred most frequently in large colonies (Table 1). The smallest colony with a communal egg dump had 134 nests. The colony with the most communal egg dumps (14) also had the most nests (4,721). The number of nests and the number of communal egg dumps in colonies were significantly positively correlated ($r_s$ = 0.43, $P < 0.001$, n = 150). Some communal egg dumps were closely spaced. Three (with 13, 13, and 22 eggs) were within 12 m of each other and two of these (with 13 and 13 eggs) were 4 m apart in a colony of 844 nests. Another three (with 12, 13, and 14 eggs) were within 16 m of each other and two of these (with 13 and 14 eggs) were 4 m apart in a colony of 2,079 nests.

We documented the rate of increase or decrease in the number of eggs in several communal egg dumps. The number of eggs in a nest with 15 eggs increased to 19 by the following day at a rate of four eggs/d (the maximum rate recorded). The largest communal egg dump had 26 eggs on 15 July, 30 eggs (including fragments of one) on 19 July (Fig. 2), 31 eggs (including fragments of one) on 22 July, and 24 eggs on 29 July 2013. The number of eggs in this nest increased at a rate of 0.71 eggs/d and then decreased at a rate of 1.0 egg/d. In contrast, the communal egg dump with 18 eggs guarded by the Clark's Grebe had the same number of eggs when inspected 7 d later. The number of eggs in a nest with 11 eggs declined to four eggs 2 d later at a rate of 3.5 eggs/d, and all eggs disappeared 3 d later.

Our motion-activated cameras frequently documented frenzied copulation and occasional egg laying by grebes, during both day and night, on nests recently abandoned due to egg predation by mammals or transportation of nests to shallow water by wind-generated waves. In some cases, both species of grebes copulated and laid eggs on the same nest. Usually, the eggs on these nests

**Table 1**. Relationship between colony size and number of communal egg dumps (> 10 eggs in nest) for the Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) at Clear Lake, California, during 2010–2019.

| Number of nests in colony | Number of colonies | Number of egg dumps | Number of egg dumps per colony |
|---|---|---|---|
| 1–99 | 109 | 0 | 0 |
| 100–199 | 9 | 2 | 0.22 |
| 200–299 | 5 | 1 | 0.20 |
| 300–499 | 11 | 3 | 0.27 |
| 500–999 | 8 | 11 | 1.38 |
| 1,000–4,721 | 8 | 34 | 4.25 |

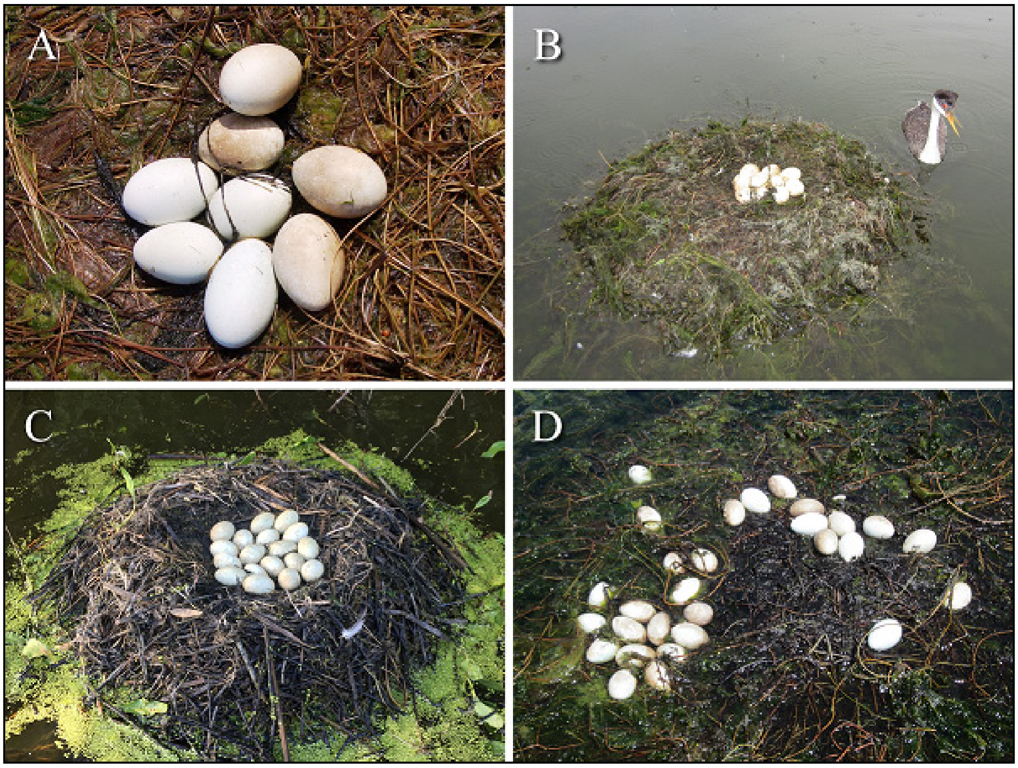


**Figure 2**. Examples of brood parasitism in Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) at Clear Lake, California. (A) A well-maintained nest with four pale eggs recently laid by a presumed brood parasite in a nest with four brown-stained eggs previously laid by a host. (B) A male Western Grebe vigorously defending 10 eggs in a well-maintained nest. (C) A well-maintained nest with 18 eggs incubated by a male Clark's Grebe and female Western Grebe. (D) An unmaintained nest with 30 eggs, including fragments of one egg (a 31st egg was present 2 d later). (Photographed by Floyd E. Hayes).

were not incubated but sometimes they were incubated intermittently. Two cameras documented an unusual instance of egg dumping after a windstorm on 18 July 2015, when numerous nests with at least 11 visible eggs were transported to shallow water. Although the grebes stopped incubating eggs in these nests, 25 copulations on at least five different nests were recorded during the next 7 h, two the following night, and four the following day. The grebes also dumped new eggs in the abandoned nests, with the number of visible eggs increasing from 11 to 13 during day 1, 17 eggs by day 4, and 20 eggs by day 5, with up to 11 eggs on a nest. None of the eggs were subsequently incubated and all gradually sank underwater as the nests disintegrated.

## Discussion

Disturbance of nesting birds by researchers may negatively impact their breeding success (Fair et al. 2010). Our 2010 and 2019 surveys of clutch size in three large colonies and our repeated visits in 2010 to count eggs in marked nests at one colony did not result in colony abandonment, which often happens on Clear Lake for no apparent reason (Hayes et al. 2022). The number of days of our monitoring effort per breeding season varied by more than four-fold and was not significantly correlated with the number of nests, number of young, number of young per nest, or the productivity ratio of young to adults (Hayes et al. 2022). The number of young per nest, which we consider the best measurement of reproductive successive, was the second highest in 2010 and fourth highest in 2019 during our 10-y study (Hayes et al. 2022). These results indicate that our intrusions into colonies to count eggs in 2010 and 2019 did not significantly reduce breeding success.

The mean clutch size of typical grebe nests in the two 2010 colonies (2.29–2.37) is similar to previous reports from Clear Lake (2.10–2.40; Feerer and Garrett 1977) and Utah (2.6; Lindvall and Low 1982). The mean clutch size of the 2019 colony was much higher (3.12) but still lower than previous reports from British Columbia (up to 3.7; Forbes 1988), Colorado (up to 3.89; Davis 1961), and Manitoba (up to 4.2; LaPorte et al. 2014). Although only 3% of our nests contained > four eggs in the two 2010 colonies, up to 12.2% of nests contained > four eggs in Manitoba (http://birdsoftheworld.org/bow/species/wesgre), 13.7% in British Columbia (Forbes 1988), 15.2% in our 2019 colony, and 39.1% in Colorado (Davis 1961).

Our study provides new data on the maximum number of eggs incubated by the grebes. Lindvall and Low (1982) reported that clutches with > four eggs in Utah were not incubated. Forbes (1988) stated that all 19 clutches with > four eggs in British Columbia were incubated, but did not provide a maximum clutch size. LaPorte et al. (2014) reported that clutches with > six eggs in Manitoba were always cold and presumed abandoned. We occasionally observed grebes incubating clutches of up to 10 eggs, however, and in one case we observed a mixed pair of grebes incubating 18 eggs in a well-maintained nest (Fig. 2).

Our observations reveal that eggs frequently disappear and reappear on nests of all clutch sizes. New eggs appearing on nests well after the eggs of the initial host were laid provide evidence of brood parasitism. We provide the estimates of the daily rate of brood parasitism for these species, with a rate much higher (2.6–10.4% of nests/d) than the only previously published total rate of 1.8% of Western Grebe nests (Nuechterlein in Rohwer and Freeman 1989). Although our sample sizes are small, the daily rate of brood parasitism was lower for nests with 1–4 eggs than for nests with 15–31 eggs. Our methods did not exclude the possibility of parasitic eggs being laid prior to the last egg laid by the parents incubating the eggs. Brood parasites should have a stronger incentive to parasitize nests at an early period of the egg-laying cycle of a host, especially for species such as grebes with asynchronous egg laying and hatching because eggs laid earlier are more likely to hatch and less likely to be abandoned (Konter 2011).

The grebes appeared to be especially attracted to abandoned nests with failed clutches due to predation or windstorms. Because floating grebe nests are a valuable resource requiring considerable time and energy to construct and maintain daily to prevent disintegration in the water (Fjeldså 2004), the nests were frequently reused by the grebes for copulation, egg laying, and sometimes for incubation of laid eggs (Hayes and Turner 2017; Hayes et al. 2018a,b). Konter (2008) similarly reported an increase in egg parasitism on nests of the Great Crested Grebe after many eggs were destroyed by a storm. Brood parasites are presumably more successful in parasitizing abandoned nests than active nests because abandoned nests are not defended by a mated pair. The eggs laid in abandoned nests, however, are less likely to be incubated than those in active nests.

Communal egg dumping is probably initiated in abandoned nests with failed clutches, although the mixed pair incubating 18 eggs in a well-maintained nest may have been an exception. The large communal egg dumps of the Western Grebe and Clark's Grebe are unique among grebes (Fjeldså 2004). Our maximum count of 31 unincubated eggs in a nest nearly doubled the previously reported high of 16 eggs (Finley 1907). The maximum number of eggs reported in nests of other grebe species is 11 in the brood parasitic Great Crested Grebe (Moskal and Marszałek 1986) and non-brood parasitic Pied-billed Grebe (*Podilymbus podiceps*; Lee et al. 2008). Our data reveal that egg dumping is more likely to occur in larger colonies, where more nests with failed clutches are available. Hill et al. (1997) reported brood parasitism to be more common in a high-density colony than in a low-density colony of Eared Grebes. Konter (2008) reported that the largest clutches of the Great Crested Grebe, which presumably included parasitized eggs, occurred in areas of a colony with high nest density.

Grebes are indeterminate and prolific egg layers. The Horned Grebe (*Podiceps auritus*) can lay up to 50 eggs in a season (Fjeldså 2004), the Least Grebe (*Tachybaptus dominicus*) can lay up to 35 eggs during a breeding season (Gross 1949), and the Pied-billed Grebe can lay up to 13 eggs in 15 d (Fugle and Rothstein 1977). The Western Grebe and Clark's Grebe also appear to be prolific egg layers, frequently laying eggs in the nest of each other whether attended or unattended, and the Western Grebe has been reported parasitizing a nest of the Red-necked Grebe (*Podiceps grisegena*; Van Damme 2004, 2006). The rate of heterospecific brood parasitism remains unknown but could be documented by studying the DNA of eggs. It is unknown whether parasitic eggs are laid by unmated young females, mated females with active clutches, mated females with failed clutches, or a mixture of these groups. It is also unknown what proportion of females engage in brood parasitism. Given their ability to produce many eggs, it is possible that all females engage in brood parasitism.

Some species of birds react aggressively to conspecific brood parasites by removing parasitic eggs or hatchlings from their nests to reduce the costs of raising unrelated offspring. The best known example among grebes is the Eared Grebe, in which eggs are often destroyed, presumably by conspecifics (McAllister 1958), with a higher rate of egg loss and infanticide occurring in parasitized nests than in non-parasitized nests (Lyon and Everding 1996). In contrast, egg destruction is rare in the Western Grebe and Clark's Grebe (Hayes et al. 2018b) and infanticide has never been documented. These grebes respond more passively to brood parasites and tolerate the accumulation of more parasitic eggs in nests. Conspecific and interspecific brood parasitism by females of the two species is more extensive than previously realized and appears to be a common and adaptive reproductive strategy that potentially increases the probability of producing additional offspring without incurring the extra costs of parental care. Even though eggs dumped in failed nests are unlikely to be incubated, the incubation of 18 eggs by a mixed pair of grebes for at least 7 d indicates that there is always a chance, even if small, that dumped eggs will be incubated and the hatchlings raised by other grebes.

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