High frequency of conspecific brood parasitism in a colonial waterbird, the Eared Grebe *Podiceps nigricollis*

Bruce E. Lyon and Susanne Everding

We made daily visits to 47 Eared Grebe *Podiceps nigricollis* nests in two colonies to determine the frequency of conspecific brood parasitism. Three criteria were used to detect parasitism: the appearance of two or more new eggs in a 24 hour period, new eggs after the host had ceased laying, and the disappearance of a marked egg with the simultaneous appearance of a new unmarked egg. We detected parasitism at 68% of nests in one colony, 14% of nests in the second colony, and 38% of nests in both colonies combined. The spatial dispersion of parasitic eggs among host nests within one colony did not differ from random expectation but, with respect to temporal dispersion, parasites were more likely to lay in host nests in the laying stage than expected by chance. Egg loss was more common at parasitized nests than unparasitized nests, but further studies are needed to confirm whether this is due to egg rejection by hosts. A comparison of clutch sizes in parasitized and unparasitized nests indicated that unparasitized nests never contained more that four eggs – supernormal clutches of five or more eggs thus indicate that parasitism has taken place and, if used as an assay for parasitism, would have identified two thirds of the cases of parasitism in our study. Applying this assay to clutch size information collected 40 years ago at a site close to our study area indicates that parasitism may be a regular feature of Eared Grebe reproduction.

B. E. Lyon (correspondence), Kananaskis Field Stations, Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4. S. Everding, Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6. E-mail: blyon@acs.ucalgary.ca

Conspecific brood parasitism (CBP) has now been reported in over 150 species of birds, and encompasses diverse taxonomic groups and life histories (Yom-Tov 1980, Rohwer and Freeman 1989). CBP, however, remains a poorly understood reproductive behavior, largely due to difficulties in identifying individual parasitic females. Two important issues have been addressed when seeking an understanding for the occurrence of CBP, each relying on a different methodology.

First, a number of adaptive hypotheses have been proposed to explain why females lay eggs in the nests of conspecifics (Andersson 1984, Gibbons 1986, Eadie et al. 1988). Field studies conducted to date indicate that parasites tend to be either females that are unable to nest because they lack the body condition or resources necessary for nesting (Eadie 1989, Lank et al. 1989) or they are nesting females who lay eggs in neighboring nests to bypass parental care constraints and increase their reproductive success (e.g. Gibbons 1986, Jackson 1993, Lyon 1993a).

The second issue concerns the variation among species in the frequency of parasitism: why is parasitism common in some species and absent in others? Explanations for this comparative pattern fall into two broad categories, opportunity and constraint (Eadie 1991). For example, species may differ in factors that influence the cost-benefit trade-offs of parasitism or in factors that influence the opportunity to lay eggs in the nests of other females. Comparative data suggest that both the opportunity to lay parasitically and the benefits derived from parasitism can influence the frequency of parasitism. For example, one particularly important corre-

late of parasitism is colonial breeding (Andersson 1984, Håland 1986), presumably due to the abundance of potential hosts in colonies. Parasitism is also particularly common in precocial birds (mainly Anseriformes and Galliformes; Yom-Tov 1980, Eadie et al. 1988, Rohwer and Freeman 1989) and it has been suggested that this is due to the high success rate of parasitic eggs in precocial birds (Sorenson 1992). However, there is still debate over the interpretation of these patterns (Rohwer and Freeman 1992, Sorenson 1992), and much of the interspecific variation in the occurrence of CBP is unexplained.

Part of the problem with these comparative analyses is a lack of information. Although it is clear when parasitism occurs in a species, it is less clear when it does not occur. A lack of evidence for CBP could be due to the fact that it does not occur, or because the type of detailed field study needed to document its occurrence has yet to be conducted (Lyon et al. 1992). Detailed field studies are needed from a large number of taxonomic groups to obtain the information necessary for a comprehensive understanding of the taxonomic and ecological distribution of this life history tactic.

We studied the Eared (Black-necked) Grebe *Podiceps nigricollis* to determine the occurrence and frequency of CBP in this colonial species. Parasitism has been reported for two other species of grebes (*Podiceps cristatus, P. griseigena*; Cramp 1977), but only as rare events and not as a regularly occurring reproductive tactic. CBP has not been reported in Eared Grebes. We also examined patterns of egg laying and egg loss to determine whether host choice by parasites or defensive behaviors by hosts might occur in this species.

Methods

We studied nesting Eared Grebes from 4 June to 28 June, 1988, at Jaimeson Meadow, a Ducks Unlimited managed wetland, near Big Creek, British Columbia, Canada. Hardstem bulrush *Scirpus acutus*, the predominant emergent plant at this wetland, is limited to a thin strip along some shorelines and a few sparse patches away from shore. We studied two grebe colonies. Colony 1 was located away from emergent vegetation and nests were anchored to submergent vegetation. The nesting density in Colony 1 was extremely high and most nests were within 1–2 m of four to five other nests. Colony 2 was located about 200 m from Colony 1 in very sparse patches of bulrush, where the vegetation provided an anchor for some of the nests, but not protective cover. Nest density at Colony 2 was much lower than Colony 1, and most nests had one or two neighbors within 2 m, and often none.

To monitor the occurrence of parasitism, we checked nests daily at Colony 1 from 4–20 June and daily at Colony 2 from 15–28 June, except for 21 June. This sample yielded 249 nest-days of observations for Colony 1 and 214 nest-days of observations for Colony 2. Each nest was marked with numbered flagging tape attached under the water surface to the stems of emergent or submergent vegetation. We used three criteria to determine if parasitism had occurred: the appearance of two or more eggs on the same day (criterion 1), the appearance of new eggs after clutch completion (criterion 2), or the disappearance of a marked egg with its simultaneous replacement with an unmarked egg (criterion 3). Most of the cases of parasitism were detected by the first criterion. Given that nests were checked daily and that most nests were found when they contained their first egg, the first criterion would be very accurate (Frederick and Shields 1986), although it would tend to underestimate parasitism slightly. For the second criterion, we assumed that any new eggs laid after a non-laying interval of three or more days was a parasitic egg. We based this decision on the observed laying pattern of the grebes in their own nests: eggs were regularly laid at either one or two day intervals, but almost never at three day intervals over the laying period. A possible problem with the third criterion is that it would falsely indicate parasitism whenever identification markings on an egg had disappeared. Since grebe eggs are often covered with damp nest vegetation and therefore wet, they can be difficult to mark with an indelible pen, and criterion 3 may not be accurate. However, very few of the cases of parasitism we detected depended on this criterion (see below).

When estimating the frequency of parasitized nests at Colony 2 we omitted four nests that were observed for at most over a four day period, and one nest that contained three eggs when first found, as we could not be sure that these nests were never parasitized. Calculations of clutch sizes for parasitized and unparasitized nests excluded nests that were depredated or abandoned before clutch completion or nests that were not observed for at least three days after the last new host egg was laid. Values reported with means are standard errors and G-statistics have been adjusted with William's correction (Sokal and Rohlf 1981).

As part of a separate pilot study on parental care and parent-offspring interactions in Eared Grebes, we conducted approximately 30 h of observations on unmarked grebe broods at two wetlands; Jaimeson Meadow (1988, 1989) and Pond 40 at Riske Creek (1992). Observations were made at close range (5–10 m) from floating blinds and we were able to observe the number of adults present with each brood, brood size, size differences among chicks, parental feeding of chicks, and interactions among chicks. We draw upon these observations to consider how parental care con-

straints on brood size might explain the occurrence of brood parasitism.

Results

Frequency of parasitism

Parasitism was extremely common in Colony 1, with 68.4% of the 19 nests parasitized. Parasitism was less common in Colony 2 and 14.3% of the 28 nests were parasitized. Overall, 17 parasitized nests were detected (38.3% of all nests).

The accuracy of these frequency estimates depends on the criteria used to assess parasitism. Since we detected most cases of parasitism using the appearance of two or more eggs in a nest on the same visit (22 of 28 eggs) our estimates of parasitism rates should be fairly accurate. An additional two parasitic eggs were detected based on appearance after clutch completion (3 and 4 d after completion, respectively), but this was in a nest where parasitism was independently detected during laying. Finally, the remaining four parasitic eggs were detected based on the disappearance of a marked egg with the simultaneous replacement with an unmarked egg, the least reliable method. However, two of these eggs were in nests that were independently identified as parasitized nests based on the appearance of two or more new eggs per day. Thus, in terms of the frequency of parasitized nests, only two of the 17 parasitized nests were identified solely by criterion 3 and no parasitized nests were identified solely by criterion 2.

The occurrence of supernormal clutches has been used in some studies as evidence for parasitism (Yom-Tov 1980, Eadie 1991). In this study, clutches were significantly larger in parasitized nests than in unparasitized nests (Fig 1; 5.67 ± 0.51 eggs versus 3.32 ± 0.13 eggs; $t = 5.50$, $P < 0.001$). However, the number of eggs laid by the host in parasitized nests (3.93 ± 0.41 eggs) did not differ from the mean clutch size in unparasitized nests (3.32 eggs; $t = 1.74$, $P = 0.09$).
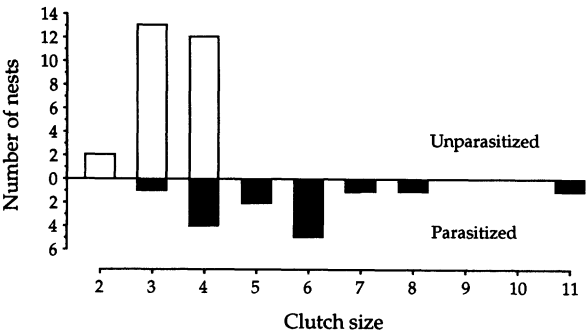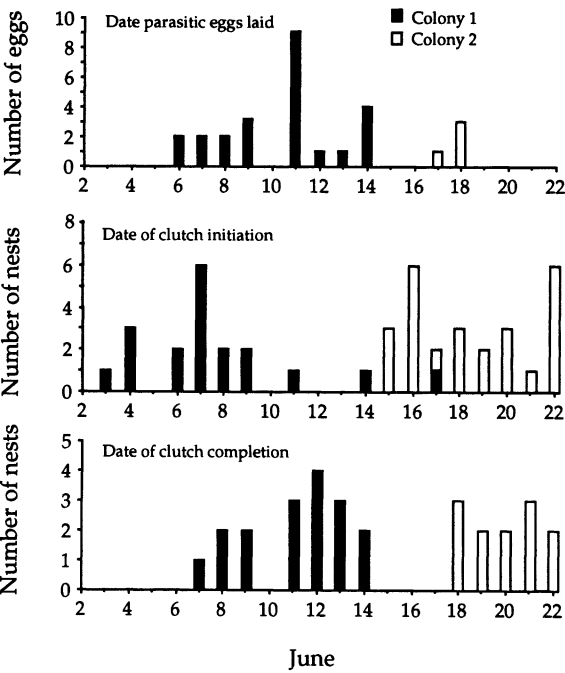

Fig. 2. Phenology of parasitic egg-laying (top) relative to clutch initiation dates (middle) and clutch completion dates (bottom) for Colony 1 and Colony 2.

All of the 25 unparasitized nests had clutches of four or fewer eggs while 66.7% of the parasitized nests contained five or more eggs (Fig. 1). Thus, using a clutch size of four eggs as the cutoff to identify parasitized nests would have correctly identified two thirds of the cases of parasitism in the 15 parasitized nests that reached clutch completion and would not have falsely indicated any cases of parasitism.

The average date of clutch initiation was earlier at Colony 1 than Colony 2 and, with the exception of one renest at Colony 1 on 17 June, there was no overlap in the dates of initiation at the two colonies (Fig. 2). The chronology of parasitic laying at Colony 1 largely spanned the period over which the colony contained nests at the laying stage, while the few cases of parasitic laying at Colony 2 all occurred early on (Fig. 2).

Are host nests a random sample with respect to breeding cycle?

Most of the parasitic eggs were laid in host nests that were at the laying stage (26 of 28 eggs). This could reflect non-random host choice by parasites or it could also result from random laying when breeding is very synchronous (Lyon 1993b). To distinguish between these two hypotheses, one must consider whether the distribution of parasitism differs from random *given* the host nests available to parasitic females when each

Fig. 1. Clutch sizes in parasitized and unparasitized nests.

240

parasitic egg was laid. We therefore ran a Monte Carlo simulation to determine whether the observed pattern deviated from random expectation, given the relative number of potential host nests at the laying versus incubation stage on the day each parasitic egg was laid. Our analysis is restricted to Colony 1 because all 24 eggs at Colony 1 were laid on days when nests at both the laying and incubation stage were available as potential host nests, whereas only nests at the laying stage were available when the four parasitic eggs at Colony 2 were laid. For each parasitic egg, a host nest was chosen at random from the pool of all available host nests (any nest that was active on the day the egg was laid), the total number of eggs laid in a host nest at the laying stage was calculated at the end of each run, and this process was repeated 1000 times to yield a probability distribution. Based on the simulation, the observed pattern of 22 of 24 parasitic eggs being laid in host nests at the laying stage was non-random (two-tailed $P < 0.001$; expected value is 16.4 eggs laid in nests at the laying stage).

Number of parasitic eggs per nest: clumped, uniform or random distribution?

Of the 17 parasitized nests, 12 nests received a single egg, one nest received two eggs, two nests received three eggs and two nests received four eggs. Although some cases of multiple laying would be expected under random laying, deviations from random distributions could be expected if: (i) parasitic females lay several eggs in the same host nest (clumped expectation), (ii) some nests are more vulnerable or sought after as hosts and are parasitized by several females (clumped expectation), or (iii) females tended to avoid laying in nests that had already been parasitized (uniform expectation).

The temporal pattern of laying indicates that most of the observed cases of multiple laying were not due to a single parasite laying several eggs in the same host nest, but due mainly to more than one female each laying a single egg in the same host nest. Of the 16 eggs involved in multiple-laying, 12 were laid on the same night as the other parasitic eggs laid in the same host nests (4 nests where 2 eggs were laid on the same day, 1 nest where 4 eggs were laid on the same day). Thus, most cases of multiple laying in a host nest were due to different females and did not involve individual parasites laying several eggs in the same host nest.

Having ruled out one possible explanation for why a clumped distribution might occur, the question remains as to whether the dispersion of eggs actually deviates from random expectation. We used Monte Carlo simulations to answer this question. Since so little parasitism, and no multiple laying, occurred at Colony 2, we restricted the simulation to Colony 1. In the simula-

tion, each of the 24 parasitic eggs was distributed randomly among the potential host nests available to them on the night they were laid. For the 22 eggs laid in nests at the laying stage, only nests at the laying stage were considered as potential hosts, but for the two eggs laid in host nests at the incubation stage, all nests with eggs were considered as potential host nests. At the end of each run, we tallied the number of eggs that were laid together in host nests with at least one other parasitic egg, and then repeated this process 1000 times to obtain a probability distribution for the observed pattern. This process revealed that the observed pattern, 16 parasitic eggs laid together in a host nest with at least one other parasitic egg, could have occurred with random laying (two-tailed $P = 0.59$; expected value of 17.6 eggs laid in nests with ≥ 1 other parasitic egg).

Egg loss and parasitism

During our census of nests we noticed that egg loss was fairly common, including both partial and total loss of clutches. Such loss could be due to hosts rejecting eggs, parasites removing eggs during parasitism or desertion of parasitized nests with the subsequent destruction of the undefended eggs. To distinguish such possibilities from simply a high loss rate of eggs at all nests, we compared the loss rate for parasitized nests and unparasitized nests. A significantly higher proportion of parasitized nests lost eggs (13 of 17 nests lost some or all of their eggs) than did unparasitized nests (9 of 28 nests; $G_{adj} = 8.3$, $P < 0.01$). For the parasitized nests that lost eggs, six nests lost all of their eggs suddenly (although laying at two of these continued the following day, with full-sized clutches eventually being laid), two nests lost all of their eggs over a period of several days and five nests lost part of their clutch. Of the 50 eggs that disappeared from parasitized nests, 43 disappeared after parasitism first occurred, one before it occurred and six on the same day that a parasitic eggs was laid. Note, however, that five of the six cases where the eggs disappeared on the same day that parasitism occurred involved the four cases of parasitism identified by criterion 3, the least reliable method of detecting parasitism. In these cases, it is possible that markings came off eggs rather than eggs being lost.

Discussion

We found a high frequency of brood parasitism in the population of Eared Grebes we studied, although this was due to extraordinarily high levels at one of the two colonies, not a uniformly high level of parasitism at both colonies. Nonetheless, the average proportion of nests parasitized at both colonies combined is greater

than the frequencies reported for virtually all previous studies involving non-waterfowl species, and the levels at Colony 1 exceed virtually all values previously for birds, including waterfowl, which have higher rates of parasitism than other birds (Rohwer and Freeman 1989). In addition, our estimates of the rates of parasitism may be slight underestimates, for two reasons. First, some nesting females laid eggs in their nests every day, but others appeared to lay every second day and, when parasitism occurred on the day the host skipped, such cases would not have been detected by criterion 1. Second, there were several instances where single eggs were laid in inactive nests and many or all of these could have been cases of parasitism, but they were not counted as such.

With such a small sample of colonies in our study, we can only speculate as to why parasitism occurred at such a high frequency at Colony 1. Nesting density may be important. Of seven grebe colonies we visited in the region between 1987 and 1992, Colony 1 had, by far, the highest density of nests. It is unclear why density per se should matter in a colonial species, because the arguments that have been used to explain why parasitism is more common in colonial species should apply to both high and lower density colonies. These explanations include the ease of locating nests, the lack of territorial defence and the abundance of host nests in colonies (Hamilton and Orians 1965, Brown 1984, Håland 1986). However, one possible explanation for a density effect is that it may be more difficult for birds to defend their nests effectively at extreme densities, as there are often several pairs of neighbors at close proximity. During the brief observations we made from a floating blind during the egg-laying period at Colony 1 (a 1 h observation period) we saw constant interactions, with numerous threats, chases, and several birds climbing onto nests that were apparently not their own, as they were vigorously chased from those nests. Other studies have also found that hostile interactions, like chases and threats, are common during laying in Eared Grebe colonies (McAllister 1958). Such constant social interaction may leave nests temporarily vulnerable to parasitism by other grebes. Behavioral observations at colonies during laying would be most interesting.

We found that the occurrence of a supernormal clutch (> 4 eggs) indicates that parasitism has occurred with certainty in the population we studied and, when used as the sole assay for parasitism, would have identified two thirds of the cases of parasitism. Using this information, we can estimate the frequency of parasitism in populations of grebes studied in the same region as our study (within 100 km) 40 years ago (McAllister 1958). Of the 293 nests studied, 20 contained more than four eggs, indicating that roughly 30 nests, or 10.2% of the total, were parasitized (McAllister 1958). However, most of the supernormal clutches she observed occurred at one colony studied in 1955, where 12 of 113 nests had supernormal clutches (estimated frequency of parasitism; 15.9%).

These estimates are likely to be low because the clutch sizes reported did not include eggs that were removed from nests due to egg loss (McAllister 1958). In some colonies, egg loss occurred at most nests, often the first eggs laid (McAllister 1958), and had these eggs been included when calculating total clutch size, as they were in our study, the estimated rate of parasitism would be much higher. In addition, McAllister noted many instances where single eggs were laid in nests that were abandoned. She referred to these eggs, and to the early eggs that were tossed from nests, as 'yard eggs' that result from physiological miscue between the timing of laying and the benefits of extreme synchronous breeding within colonies. However, given our observations, many of these 'yard eggs' were likely instances of brood parasitism. Regardless, it is clear that brood parasitism is a regular feature of Eared Grebe colonies in central British Columbia.

Without information on the identities of the parasitic females, the reasons for why female Eared Grebes are parasitic will have to await future studies. However, aspects of the biology of this species strongly suggest that some explanations are more likely than others. As a colonial species, territories or nest sites are unlikely to be limiting. It is therefore unlikely that parasites are females that are unable to breed in a given year (e.g. Eadie 1991, Lyon 1993a). Although egg loss is common, nest predation appears to be very rare (Boe 1993, this study) and only two partial clutches were preyed on during the period of parasitic egg-laying. Thus, most parasitism was not a response to the destruction of partially complete clutches.

The most likely explanation is that most parasitism is by nesting females who lay additional eggs in the nests of other pairs. By laying extra eggs in the nests of conspecifics, nesting females could bypass parental care constraints on brood size and increase their reproductive success. As indeterminate egg-layers, female Eared Grebes are physiologically capable of laying more eggs than the typical clutch size in a continuous laying sequence (McAllister 1958); nesting females could thus lay parasitically without sacrificing their own clutch sizes. However, laying these extra eggs parasitically, rather than in their own nests, would only make sense if parental care limited the brood size that birds could raise in their own nests (Lyon 1992, 1993a, Jackson 1993).

Observations of grebe broods at the study area indicate that food for chicks is likely to be an important constraint on brood size (Lyon, personal observations). After hatching, the chicks are carried on their parents' backs to foraging areas, and there they are fed aquatic invertebrates by both parents. For at least the first week, the chicks do not capture their own food and depend entirely on their parents for food. Strong differ-

ences in body size develop among the chicks in a brood, possibly due to hatching asynchrony, and physical aggression among broodmates is common. Although many broods initially hatch with three or four chicks, many broods are eventually reduced to two chicks, with a single chick tended by each parent. Given the size differences and aggression among chicks, this brood reduction is likely the result of starvation (Lack 1947). Taken together, these observations suggest that food ultimately limits the brood sizes that parent grebes can raise – parasitism would allow females to circumvent these constraints and increase their reproductive success at the expense of the hosts they parasitize. Moreover, the brood observations also revealed that family units invariably consisted of two parents, indicating that when two female grebes lay in the same nest it is brood parasitism, not joint-nesting involving two females and a male (e.g., Gibbons 1986).

Parasitism by nesting females has been observed in several other species, and the females either laid parasitically prior to initiating their own clutches (Gibbons 1986, Lyon 1993a) or after completing their clutches (Møller 1989), and most parasitic eggs were laid in a continuous sequence with their own eggs. If this were true in Eared Grebes, we would expect to see instances of parasitism either directly preceding clutch initiation or directly following clutch completion of nesting females. While some of the patterns of laying are consistent with this (Fig. 2), most are not. For example, the pulse of parasitic laying on 11 June is associated with neither a pulse of clutch initiation nor completion (Fig. 2). Alternatively, parasites might lay several eggs, possibly a full clutch, and then initiate their own nests after an interval of some time (Sorenson 1991). The observations that the first parasitic eggs laid at Colony 1 involved two eggs per day over a four day period (Fig. 2; excluding a third dubious case on 9 June detected by criterion 3) is consistent with two females each laying a typical full clutch of four eggs parasitically, one egg per day. That these eggs were laid in six host nests rules out the possibility that these were actually instances of joint-nesting rather than parasitism (e.g., Gibbons 1986). It is also possible that many of the parasitic eggs laid in nests in Colony 1 were laid by females that eventually nested in Colony 2.

Whenever parasitism is a regular feature of the reproductive ecology of a species, the evolution of parasitic tactics that enhance the success of parasitic eggs, and of defensive counter tactics by hosts to reduce the costs of parasitism, might be expected. We observed two possible candidates, non-random host use and a high loss rate of eggs at parasitized nests. A Monte Carlo simulation demonstrated that significantly more parasitic eggs were laid in nests at the laying stage than would be expected under random laying, a tactic that would increase the hatching success of parasitic eggs. This pattern has been observed in other species as well

(Emlen and Wrege 1986, Brown and Brown 1989), but it has also been notably absent in others (Gibbons 1986, Lyon 1993b). Interestingly, the three species that show non-random host choice are all colonial (including this study), while the two lacking it are territorial. Observations in these studies indicate that the colonial species have a much larger pool of potential hosts to choose from than the territorial species – lack of hosts may constrain adaptive host choice options for territorial brood parasites. An alternative explanation for these patterns of non-random host use is that nests in colonies may be more vulnerable to parasitism during laying, possibly because they are left unattended for longer periods, and not because parasites are gathering information about the stages of nests and choosing accordingly. Behavioral observations of hosts and parasites are needed to fully resolve this issue.

We also observed a high rate of egg loss associated with parasitism, and this included both total and partial clutch loss. Some cases of total loss may have been cases where hosts deserted their nests following parasitism (McRae 1995), followed by the removal of these unprotected eggs by other conspecifics or predators. Partial loss could be due either to egg rejection by hosts or to removal by parasites. Removal by parasites seems unlikely because 88% of the removals occurred after parasitism had occurred, and most of the 10% of the cases that occurred during parasitism involved the dubious cases of parasitism identified by criterion 3. Thus, it appears that the partial egg loss was due to hosts.

Partial egg loss may therefore represent adaptive egg rejection by hosts, a defensive host tactic observed in other species (Victoria 1972, Lyon 1992). We were unable to determine whether the eggs that disappeared at nests with partial egg loss were parasitic eggs, as would be required if egg loss were due to egg rejection by hosts, because grebe eggs are immaculate white and lack the types of markings that have been used to distinguish parasitic eggs from host eggs in other studies (e.g. Victoria 1972, Gibbons 1986, Jackson 1993, Lyon 1993a). However, if egg rejection does occur in Eared Grebes, the fact that their eggs lack markings indicates that hosts cannot be using such markings to distinguish parasitic eggs from their own (e.g. Victoria 1972). Instead, recognition and rejection would likely be based on egg shape, as has been observed for a host of an interspecific brood parasite (Mason and Rothstein 1986).

Conclusions

We have shown that CBP can be very common in some colonies of Eared Grebes, and estimates from an earlier study suggest that our observations are not unique. We suggest that this species would be an ideal species for

continued work on various aspects of CBP because (i) they are exceptionally tame when approached with a floating blind and can be observed from close distance, (ii) egg-laying often occurs during the daytime (McAllister 1958) so that behavioral observations during parasitism could be made, and (iii) in dense colonies, large numbers of nests and individuals could be monitored at the same time and, with high rates of parasitism, a large number of parasitic events could be observed. Such observations would also indicate whether parasites are actively choosing host nests in the laying stage or simply parasitizing nests on the basis of their availability. In addition, egg rejection is rare in species with conspecific brood parasitism (Lyon 1992) and confirming its occurrence in grebes, and identifying the mechanisms involved, would be worthwhile.

References

Andersson, M. 1984. Brood parasitism within species. – In: Barnard, C. J. (Ed.) Producers and Scroungers. Croom Helm, London, pp. 195–228.

Boe, J. S. 1993. Colony site selection in eared grebes in Minnesota. – Col. Waterbirds 16: 28–38.

Brown, C. R. 1984. Laying eggs in a neighbor's nest: benefit and cost of colonial nesting in swallows. – Science 224: 518–519.

– and Brown, M. B. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows. – Anim. Behav. 37: 777–796.

Cramp, S. 1977. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 1. – Oxford University Press, Oxford.

Eadie, J. M. 1989. Alternative reproductive tactics in a precocial bird: the ecology and evolution of brood parasitism in goldeneyes. – Ph. D. thesis, University of British Columbia.

– 1991. Constraint and opportunity in the evolution of brood parasitism in waterfowl. – Acta XX Congr. Int. Ornithol.: 1031–1040.

–, Kehoe, F. P. and Nudds, T. D. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. – Can. J. Zool. 66: 1709–1721.

Emlen, S. T and Wrege, P. H. 1986. Forced copulation and intra-specific parasitism: two costs of social living in the white-fronted bee-eater. – Ethology 71: 2–29.

Frederick, P. C. and Shields, M. A. 1986. Corrections for the underestimation of brood parasitism frequency derived from daily nest inspections. – J. Field Ornithol. 57: 224–226.

Gibbons, D. W. 1986. Brood parasitism and cooperative nesting in the moorhen, *Gallinula chloropus*. – Behav. Ecol. Sociobiol. 19: 221–232.

Hamilton, W. J. and Orians, G. H. 1965. Evolution of brood parasitism in altricial birds. – Condor 67: 361–382.

Håland, A. 1986. Intraspecific brood parasitism in Fieldfares *Turdus pilaris* and other passerine birds. – Fauna norv. Series C, Cinclus 9: 62–67.

Jackson, W. M. 1993. Causes of conspecific nest parasitism in the northern masked weaver. – Behav. Ecol. Sociobiol. 32: 119–126.

Lack, D. 1947. The significance of clutch size. – Ibis 89: 302–352.

Lank, D. B., Cooch, E. G., Rockwell, R. F. and Cooke, F. 1989. Environmental and demographic correlates of intraspecific nest parasitism in Lesser Snow Geese *Chen caerulescens caerulescens*. – J. Anim. Ecol. 58: 29–45.

Lyon, B. E. 1992. The ecology and evolution of conspecific brood parasitism in American coots (*Fulica americana*). – Ph.D. thesis, Princeton University, Princeton, N.J.

– 1993a. Conspecific brood parasitism as a flexible female reproductive tactic in American coots. – Anim. Behav. 46: 911–928.

– 1993b. Tactics of parasitic American coots: host choice and the pattern of egg dispersion among host nests. – Behav. Ecol. Sociobiol. 33: 87–100.

–, Hamilton, L. D. and Magrath, M. 1992. The frequency of conspecific brood parasitism and the pattern of laying determinancy in yellow-headed blackbirds. – Condor 94: 590–597.

Mason, P. and Rothstein, S. I. 1986. Coevolution and avian brood parasitism: cowbird eggs show evolutionary response to host discrimination. – Evolution 40: 1207–1224.

McAllister, N. M. 1958. Courtship, hostile behavior, nest establishment and egg laying in the eared grebe (*Podiceps caspicus*). – Auk 75: 290–311.

McRae, S. B. 1995. Temporal variation in responses to intraspecific brood parasitism in the moorhen. – Anim. Behav. 49: 1073–1088.

Møller, A. P. 1989. Intraspecific nest parasitism in the swallow *Hirundo rustica*: the importance of neighbors. – Behav. Ecol. Sociobiol. 25: 33–38.

Rohwer, F. C. and Freeman, S. 1989. The distribution of conspecific nest parasitism in birds. – Can. J. Zool. 67: 239–253.

– 1992. Why conspecific nest parasitism is more frequent in waterfowl than in other birds: a reply to M. D. Sorenson. – Can. J. Zool. 67: 1858–1866.

Sokal, R. R. and Rohlf, F. J. 1981. Biometry. – W.H. Freeman, San Francisco.

Sorenson, M. D. 1991. The functional significance of parasitic egg laying and typical nesting in redhead ducks: an analysis of individual behaviour. – Anim. Behav. 42: 771–796.

– 1992. Why is conspecific nest parasitism more frequent in waterfowl than in other birds? – Can. J. Zool. 67: 1856–1858.

Victoria, J. K. 1972. Clutch characteristics and egg discriminative ability of the African village weaverbird *Ploceus cucullatus*. – Ibis 114: 367–376.

Yom-Tov, Y. 1980. Intraspecific nest parasitism in birds. – Biol. Rev. 55: 93–108.