EGG HATCHABILITY INCREASES WITH COLONY SIZE IN CLIFF SWALLOWS

CHARLES R. BROWN AND MARY BOMBERGER BROWN

Department of Biological Sciences
University of Tulsa
Tulsa, Oklahoma 74104 USA

Abstract.—The percentage of otherwise successful nests containing ≥ 1 unhatched egg in Cliff Swallows (*Petrochelidon pyrrhonota*) varied inversely with colony size in southwestern Nebraska. Colony-site characteristics other than colony size had no significant effect on egg hatchability. The incidence of unhatched eggs at a colony site did not vary significantly with year, mean date of first egg laying, mean incubation period, extent of ectoparasitism, or mean body mass of nestlings or adults. This suggests that increased hatching failure in smaller colonies was unrelated to ectoparasitism by fleas and cimicid bugs, foraging success, or egg inattendance. Furthermore, because reproductive interference and incidence of brood parasitism do not increase in smaller colonies, these variables seem unlikely to account for the relationship between egg hatchability and colony size. More frequent matings between genetically similar individuals and reduced opportunities for females to seek extrapair fertilizations with outbred males or as fertility insurance might explain reduced egg hatchability in small colonies. Increased hatching success in larger colonies may be a benefit of coloniality for Cliff Swallows.

INCREMENTO EN LA TASA DE ECLOSIONAMIENTO CON UN AUMENTO EN EL TAMAÑO DE LA COLONIA DE *PETROCHELIDON PYRRHONOTA*

Sinopsis.—En Nebraska, el porcentaje de nidos exitosos conteniendo ≥ 1 huevos sin eclosionar de *Petrochelidon pyrrhonota* varió inversamente con el tamaño de la colonia. Fuera del tamaño de la colonia, otras características de esta no influyeron significativamente en la tasa de eclosionamíento. La incidencia de huevos que no eclosionaron en una colonia no varió significativamente con respecto al año, fecha promedio de la puesta del primer huevo, período promedio de incubación, incidencia de ectoparasitismo, ni masa promedio de pichones o adultos. Esto sugiere que el incremento en el fracaso de eclosionamiento en colonias más pequeñas no estuvo relacionado al ectoparasitismo por Siphonaptera ni por Hemiptera (Cimicidae), por el éxito de forrajeo o por el período de atención a los huevos. Más aún, dado el caso de que la interferencia reproductiva e incidencia de parasitismo reproductivo no aumentó en colonias más pequeñas, dichas variables no parecen estar directamente relacionadas con el eclosionamiento de huevos y el tamaño de la colonia. Un número mayor de apareamientos con individuos genéticamente similares y la reducida oportunidad que tienen las hembras de que sus huevos sean fecundados por machos fuera de su pareja muy bien pudiera explicar el reducido eclosionamiento en colonias pequeñas. Un incremento en el éxito de eclosionamiento en las colonias grandes pudiera ser un beneficio del colonialismo en la especie estudiada.

On average, about 10% of bird eggs fail to hatch, despite remaining intact in the nest and being incubated for the normal length of time (Koenig 1982). Hatching failure is usually attributed to either infertility or embryo mortality (Kendeigh 1942; Seel 1968; Rothstein 1973) and represents a serious fitness cost for species such as small songbirds that typically raise relatively small clutches. Few studies, however, have tried to quantify hatchability or looked for correlates with other aspects of avian population biology. An exception was Koenig (1982), whose interspecific comparison showed that hatchability in general tends to decline as species

become more social. He found that in the Acorn Woodpecker (*Melanerpes formicivorus*), hatchability is lower in larger breeding groups. If this is a general pattern among cooperative or colonial species, lowered hatchability could represent a cost of sociality not considered in previous studies of group living (Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Brown and Brown 1996). The causes of hatching failure have not been studied extensively, but possibilities include clutch neglect and consequent egg chilling, female nutrition, infertility resulting from scarcity of sperm, intraspecific brood parasitism, ectoparasitism or disease, and degree of genetic similarity (inbreeding) between parents producing a clutch (Cravens 1949; Sittman et al. 1966; Romanoff 1972; Koenig 1982; Brown and Brown 1989; Birkhead and Møller 1992; Stockley et al. 1993; Bensch et al. 1994; Kempenaers et al. 1996, 1999).

In this study we examine patterns of egg hatchability in colonially breeding Cliff Swallows (*Petrochelidon pyrrhonota*) and focus on how hatchability varies with colony size. If egg hatchability varies in any way with colony size in Cliff Swallows, it would represent a previously unidentified effect on fitness (Brown and Brown 1996) with potential consequences for the evolution of coloniality. We evaluate several possible explanations for hatching failure in Cliff Swallows and how these may be influenced by group size.

The Cliff Swallow is a 20–28 g Neotropical migrant that breeds throughout most of western North America and winters in southern South America. These insectivorous birds build gourd-shaped mud nests and place them beneath overhanging rock ledges on the sides of steep cliffs or underneath the protected eaves of artificial structures. Cliff Swallows often breed in dense colonies, and colony size within a single population varies widely. In our study area in southwestern Nebraska, mean (± SE) colony size is 393.0 (± 24.3) nests, ranging from birds that nest solitarily to colonies of 3700 nests (Brown and Brown 1996). Cliff Swallows typically have a short nesting season, 10 weeks or less in our study area, and raise only one brood (Brown and Brown 1995). In southwestern Nebraska, most birds arrive in May, and breeding is largely completed by the end of July. These birds are associated with two common ectoparasites, the hematophagous swallow bug *Oeciacus vicarius* (Hemiptera: Cimicidae) and a bird flea *Ceratophyllus celsus* (Siphonaptera: Ceratophyllidae). These insects primarily reside inside the Cliff Swallow nests or in the adjacent nesting substrate and feed on adult and nestling swallows. Swallow bugs have substantial effects on nestling survival and health (Brown and Brown 1986, 1996).

METHODS

Our research is conducted along the North and South Platte Rivers near Ogallala in primarily Keith and Garden counties, southwestern Nebraska. The study area is approximately 150 × 50 km and contains about 160 separate colony sites where Cliff Swallows breed, about 100 of which are active in any given year. These colony sites consist of both natural

cliffs along the south shore of Lake McConaughy and artificial sites such as bridges, buildings, and highway culverts on which the birds now commonly nest. Our study site is described in detail by Brown and Brown (1996).

Generally, the birds at a given bridge, culvert, or cliff face were considered a single, separate colony (Brown and Brown 1996). Residents from each site interacted with each other (for example, during foraging or when responding to a predator) but rarely interacted with birds in other culverts or bridges. In practice, each colony was a highly discrete group of nests separated from the next nearest colony by $\geq$ 3 km of habitat unsuitable for nesting. In these analyses and in our past work (Brown and Brown 1996), we consider colonies active at the same site in different years to be statistically independent. The rationale for this included the fact that environmental conditions (e.g., extent of ectoparasitism) usually changed between years, and there often was turnover among the individuals in the colonies (Brown and Brown 1996). Moreover, among the colonies included in these analyses, colony size at a site was not significantly repeatable from year to year (r_I = 0.113, P = 0.30; intraclass correlation; Zar 1999). Colony size is the maximum number of nests to have had $\geq$ 1 egg; methods of determining colony size at a site are given by Brown and Brown (1996).

Nests were checked at 1–3 d intervals from shortly before egg laying was expected to begin in a nest until either its eggs hatched or the nest failed. Nest contents were observed with a dental mirror and flashlight inserted through a nest's mud neck. Nest checks allowed us to specify the date the first egg was laid in each nest and the incubation period, defined as the number of days from the laying of the last egg to the hatching of the first egg. Once hatching date was determined, we did not check a nest again until the nestlings were 10 d old. At that time nestlings were removed, banded, and weighed, and we counted all ectoparasites present anywhere on their bodies. Body masses and parasite counts were averaged for all nestlings within a nest, and these mean values per nest were averaged to give a single measure of nestling mass and ectoparasitism per colony. Further details on how we checked nests are provided in Brown and Brown (1996). Body mass of adults was taken when nest owners at colony sites were caught in mist nets. All body-mass data for adults used in this paper came from birds caught while feeding nestlings at the end of the nesting season (see Brown and Brown 1996).

Unhatched eggs were ones still remaining when nestlings were processed at 10 days, providing a relative index of egg hatchability between colony sites. We address partial hatching failure in this paper; only nests that produced $\geq$ 1 hatchling alive to day 10 and had $\geq$ 1 unhatched egg were considered cases of hatching failure. Instances where a complete clutch failed to hatch usually resulted from abandonment or death of the nest owners and are not considered here. Because some unhatched eggs (for example, cracked ones) could have been removed by the parents before day 10, our estimates of hatching failure are probably minimum
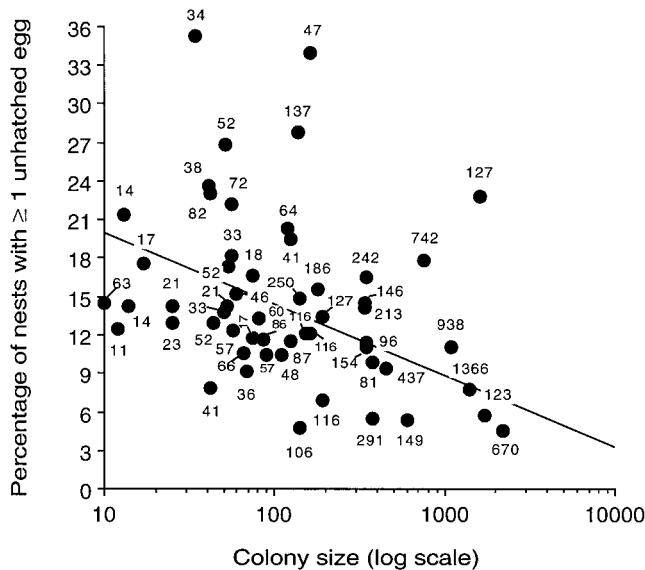
FIGURE 1.   Percentage of Cliff Swallow nests containing ≥ 1 unhatched egg in relation to
    colony size. Sample size (number of nests) for each colony is shown by dot. The per-
    centage of nests with unhatched eggs declined significantly with colony size ($r_s = -0.43$,
    $P = 0.004$, $n = 45$ colonies). Data for colonies ≤ 10 nests were combined due to small
    sample sizes.

ones. The nests with data on unhatched eggs came from 1982–1991 and
1997. For each colony, we calculated the percentage of nests with one or
more unhatched eggs, and determined the colony size (number of active
nests), mean laying date, mean incubation period, mean nestling body
mass at 10 days, mean adult body mass during feeding of nestlings, mean
number of swallow bugs per nestling, and mean number of fleas per
nestling.

RESULTS

Among all colonies and years, 11.7% of Cliff Swallow nests ($n = 8542$)
contained ≥ 1 unhatched egg. Usually a nest contained a single un-
hatched egg (8.9%); only 1.7, 0.7, and 0.4% contained 2, 3, and 4 un-
hatched eggs, respectively. Because nests with ≥ 2 unhatched eggs oc-
curred so rarely and because unhatched eggs in the same nest are prob-
ably not statistically independent events (Rothstein 1973), for the remain-
ing analyses we classified nests as having either ≥ 1 unhatched egg or no
unhatched eggs.

The percentage of nests with ≥ 1 unhatched egg declined significantly
with colony size across years (Fig. 1). The highest percentages of nests
with unhatched eggs generally occurred in colonies smaller than 200
nests, with some of these sites containing over 20% of nests with un-

TABLE 1.   Results of backward stepwise multiple linear regression of factors potentially influencing the percentage of nests with ≥ 1 unhatched egg at Cliff Swallow colony sites ($n = 44$), showing final values for each variable before removal from the regression model. Means were average values per colony site.

Variable	Standardized regression coefficient	t	P
Mean first egg laying date	−0.106	−0.256	0.81
Mean incubation period	−0.066	−0.245	0.81
Mean fleas per nestling	−0.090	−0.392	0.70
Mean adult body mass	−0.108	−0.513	0.62
Mean nestling body mass	0.028	0.142	0.89
Colony size × mean first egg laying date	0.655	0.646	0.52
Mean swallow bugs per nestling	0.165	1.055	0.30
Colony size	−0.346	−2.218	0.033

hatched eggs. When years were combined, the relationship between egg hatchability and colony size (Fig. 1) appeared to be linear; curvilinear regressions did not provide significantly better fits than linear regression (*F*-tests, $P > 0.10$ for all models tested).

The same pattern held when years were analyzed separately; in seven of eight years for which we had data from at least three colony sizes, the correlation between hatchability and colony size was negative (Spearman rank correlation coefficients of 0.36, −0.80, −0.99, −0.61, −0.70, −0.71, −0.99, and −0.50 in 1982–86, 1988–89, and 1997, respectively). This result (Fig. 1) could not be attributed to colony-site characteristics independent of colony size because site alone had no significant effect on the percentage of unhatched eggs (ANOVA, $F_{20,23} = 1.33$, $P = 0.60$); we also found no significant repeatability in egg hatchability at a site between years independent of colony size ($r_I = 0.194$, $P = 0.18$). For one site that was active in nine consecutive years (the only one with more than five years of use) and ranged from 42 to 2200 nests in size over that time, the percentage of nests with unhatched eggs varied from 17.9 to 4.5% ($r_S = −0.85$, $P = 0.004$). This single site thus paralleled the pattern seen when all colonies were combined (Fig. 1), with reduced egg hatchability when few birds nested there and greater hatchability when the colony was large.

None of the other variables measured had a significant effect on egg hatchability at a colony site. A series of Spearman rank correlations showed that hatchability was not significantly correlated with a colony's average date of first egg laying, incubation period, extent of ectoparasitism by fleas or swallow bugs, or body mass of nestlings or adults ($r_S ≥ 0.23$ for all). A backward stepwise multiple regression also showed that only the effect of colony size was significant (Table 1). We explored interactions between date of first egg laying, incubation period, extent of ectoparasitism, and body mass of nestlings and adults and found none that was significant. We found no effect of year on the percentage of unhatched eggs at a site (ANOVA; $F_{10,33} = 1.59$, $P = 0.55$), meaning this

pattern (Fig. 1) was unlikely to be an artifact of any yearly differences in how colony sizes might have been sampled.

<div align="center">DISCUSSION</div>

Cliff Swallows nesting in small colonies produced a larger percentage of unhatched eggs. To our knowledge this is the first reported case of egg hatchability increasing with breeding-colony size. All of our analyses point to colony size per se as having the single greatest influence on hatchability. We found no indication that site characteristics influenced egg hatchability independent of colony size or that hidden relationships between site and colony size across years could have accounted for these results.

Lower hatchability in smaller Cliff Swallow colonies runs counter to that seen in cooperatively breeding Acorn Woodpeckers, in which hatchability declines in larger family groups (Koenig 1982). Hatchability in woodpeckers was thought to be affected by increased reproductive interference in larger groups (Koenig 1982), but this explanation is unlikely for Cliff Swallows. Birds in smaller colonies tend to interact with each other less than do those in larger colonies (Brown and Brown 1996), and it is unclear why greater reproductive interference should necessarily lead to lower hatchability in general.

Another potential explanation for the decline in egg hatchability in smaller colonies might be that unhatched eggs represent unsuccessful cases of intraspecific brood parasitism (which Cliff Swallows frequently engage in; Brown and Brown 1989, 1996) and that parasitism is either more common or more unsuccessful in smaller colonies. Neither possibility seems likely: brood parasitism is relatively rare in small colonies, and, regardless of colony size, Cliff Swallows typically time brood parasitism to coincide with their host's nesting stage, seldom wasting eggs (Brown 1984; Brown and Brown 1988, 1989, 1996).

Hatching failure could be related to high levels of ectoparasitism by swallow bugs and fleas. This might result if ectoparasites or the pathogens associated with them impaired the physical condition of either males or females enough to reduce fertility, or (in the case of pathogens) caused embryo mortality (Romanoff 1972). However, hatchability was not significantly related to the extent of parasitism by fleas and bugs independent of colony size (Table 1). Also, if ectoparasitism accounted for higher rates of hatching failure, we should have seen lower hatchability in larger colonies that have more swallow bugs and fleas (Brown and Brown 1986, 1996), but instead we observed the opposite pattern (Fig. 1).

In the Cedar Waxwing (*Bombycilla cedrorum*), hatchability differed among habitats, with birds nearer to farms experiencing lower hatching success (Rothstein 1973). The causes were unknown, although Rothstein suggested that pesticide contamination in more agricultural landscapes could have possibly caused the differences among sites. Pesticides are suspected to cause hatching failure in nonpasserine birds (Furness and Hutton 1980). We do not know if Cliff Swallows are affected by pesticides

in this way. However, if they are, our results would imply greater pesticide contamination around small colonies which seems unlikely. There are few systematic habitat-related differences among sites that support large versus small Cliff Swallow colonies (Brown and Brown 1996, unpubl. data), and thus we doubt that birds in small colonies are exposed to potentially more pesticides than residents of large colonies. Furthermore, pesticide contamination at sites might be reflected in similar hatchability between years, with contaminated sites showing lower hatchability in successive years regardless of colony size. Yet we did not find that colony site independent of colony size had any significant effect on egg hatchability.

Female condition may at times affect egg hatchability (Cravens 1949; Romanoff 1972), and therefore increased hatching failure in small Cliff Swallow colonies might result from poorer foraging efficiency or diet quality of birds at those sites. This could occur either because birds in small colonies have less access to information from conspecifics on the whereabouts of food (Brown and Brown 1996) or because small colonies are situated in less productive foraging areas (Brown 1988). Our analyses revealed no evidence that foraging-related differences among sites were associated with egg hatchability. Average body masses of both nestlings and adults while feeding young, each an index of foraging efficiency (Brown and Brown 1996), were not significantly related to the percentage of nests with unhatched eggs at a site independent of colony size (Table 1). The absence of a date-related effect also suggests that hatching failure is unrelated to foraging efficiency: Cliff Swallows endure more frequent periods of food deprivation due to severe weather early in the season (Brown and Brown 1998), and therefore birds in early-starting colonies tend to have to fast more during the breeding season. For these reasons, it seems unlikely that food availability or foraging efficiency affect egg hatchability in Cliff Swallows.

If birds in small colonies are less efficient foragers, they might be more likely to leave their eggs unattended, resulting in chilling and embryo mortality. If this was the case, hatching failure should increase at sites where incubation periods were longer. However, average incubation period at a colony had no significant effect on the percentage of unhatched eggs there (Table 1). Cliff Swallow eggs seem to be able to withstand long periods of egg neglect during late spring cold snaps (Mayhew 1958; Brown and Brown 1995), so it seems unlikely that small differences in incubation attentiveness among colonies would account for the differences in egg hatchability. Egg chilling as an explanation also seems unlikely because of no significant date-related effects on hatchability (Table 1): colonies beginning early in the season when weather tends to be colder were not more likely to have nests with unhatched eggs than colonies starting later in the summer. Overheating of eggs during incubation seems to be as equally likely to lead to hatching failure in some birds (Kendeigh 1942; Insko 1949; Romanoff 1972), but we see no reason why eggs in small Cliff Swallow colonies would be more likely to overheat.

There were no yearly effects on hatchability, implying that particularly "warm" (or "cold") years did not affect the presence of unhatched eggs.

Could the greater incidence of unhatched eggs in smaller colonies reflect greater inbreeding in those colonies? Various studies on birds have shown that inbreeding results in greater embryo mortality and reduced hatchability, probably through a higher probability of expression of deleterious recessive alleles (Moseley and Landauer 1949; Lerner 1954; Sittman et al. 1966; Romanoff 1972; Koenig 1982; van Noordwijk and Scharloo 1981; Bensch et al. 1994; Kempenaers et al. 1996; McRae 1996). Egg hatchability is reduced even when matings are between genetically similar "non-kin" individuals who are presumably not closely related by pedigree (Bensch et al. 1994; Kempenaers et al. 1996). The overall frequency of nests with unhatched eggs in our study (11.7%) is within the range of reported levels of matings between genetically similar "non-kin" individuals in other species (Bensch et al. 1994; Kempenaers et al. 1996) but higher than most reported frequencies of matings between known close kin (e.g., Ralls et al. 1986; Rowley et al. 1993; J. Brown and E. Brown 1998; Koenig et al. 1998; cf. Hoogland 1992). While matings between kin with coefficients of relatedness of 0.25 are known in Cliff Swallows (Brown and Brown, unpubl. data), it seems more likely that any "inbreeding" in this species reflects primarily matings between genetically similar "non-kin" (sensu Bensch et al. 1994).

If small Cliff Swallow colonies are more inbred, it would be because small colonies represent more closed populations than large colonies. A smaller effective population size can lead to greater opportunity for inbreeding (reviewed in Chepko-Sade and Shields 1987; Rockwell and Barrowclough 1987; Rowley et al. 1993). In Cliff Swallows, individuals show preferences for different colony sizes, and many first-year birds return to colonies similar in size to the one in which they were raised (Brown and Brown 1996). Large Cliff Swallow colonies may also contain greater proportions of immigrants from outside the study area, with naive yearlings from elsewhere settling preferentially in larger colonies (Brown and Brown, unpubl. data). While this might increase effective population size in larger colonies and reduce the potential for inbreeding at those sites, there is as yet no strong evidence that small Cliff Swallow colonies represent more genetically closed populations than do large colonies.

Large colonies also present more opportunities for females to solicit extrapair copulations (Wagner 1993; Brown and Brown 1996). Females may copulate with extrapair males as insurance against their own mate's infertility or to avoid inbreeding (Birkhead and Møller 1992; Stockley et al. 1993; Kempenaers et al. 1996), which in either case could increase egg hatchability. Females in small Cliff Swallow colonies have fewer options to ameliorate the deleterious effects of having an infertile mate or of mating with a genetically similar male. If population structure is such that small colonies run a greater risk of inbreeding, the greater opportunities for extrapair copulation with more outbred males could be a significant advantage of breeding in larger colonies, at least for females.

Although there was no association between the presence of unhatched eggs and extrapair copulation frequency in tits, in Tree Swallows (*Tachycineta bicolor*) nests with extrapair young had higher hatching success (Kempenaers et al. 1996, 1999).

In summary, the reason(s) why egg hatchability increases with Cliff Swallow colony size are unclear. Yet, regardless of cause, the greater risk of producing eggs that fail to hatch in smaller colonies is a fitness cost that could promote formation of the larger colonies. The link in other species between inbreeding and hatching failure suggests particularly that those interested in the evolution of colonial nesting perhaps should pay more attention to the genetic structure of groups of different sizes.

LITERATURE CITED

BENSCH, S., D. HASSELQUIST, AND T. VON SCHANTZ. 1994. Genetic similarity between parents predicts hatching failure: nonincestuous inbreeding in the Great Reed Warbler? Evolution 48:317–326.

BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Sperm competition in birds. Academic, London, United Kingdom.

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

———. 1988. Enhanced foraging efficiency through information centers: a benefit of coloniality in Cliff Swallows. Ecology 69:602–613.

———, AND M. B. BROWN. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). Ecology 67:1206–1218.

———, AND ———. 1988. A new form of reproductive parasitism in Cliff Swallows. Nature 331:66–68.

———, AND ———. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. Anim. Behav. 37:777–796.

———, AND ———. 1995. Cliff Swallow (*Hirundo pyrrhonota*). No. 149, *in* A. Poole and F. Gill, eds. The birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington D.C.

———, AND ———. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, Illinois.

———, AND ———. 1998. Intense natural selection on body size and wing and tail asymmetry in Cliff Swallows during severe weather. Evolution 52:1461–1475.

BROWN, J. L., AND E. R. BROWN. 1998. Are inbred offspring less fit? Survival in a natural
    population of Mexican Jays. Behav. Ecol. 9:60–63.
CHEPKO-SADE, B. D., AND W. M. SHIELDS. 1987. The effects of dispersal and social structure
    on effective population size. Pp. 287–321, *in* B. D. Chepko-Sade, and Z. T. Halpin, eds.
    Mammalian dispersal patterns. University of Chicago Press, Chicago, Illinois.
CRAVENS, W. W. 1949. The nutrition of the breeding flock. Pp. 1–51, *in* L. W. Taylor, ed.
    Fertility and hatchability of chicken and turkey eggs. Wiley, New York.
FURNESS, R. W., AND M. HUTTON. 1980. Pollutants and impaired breeding of Great Skuas
    Catharacta skua in Britain. Ibis 122:88–94.
HOOGLAND, J. L. 1992. Levels of inbreeding among prairie dogs. Am. Nat. 139:591–602.
INSKO, W. M., JR. 1949. Physical conditions in incubation. Pp. 209–243, *in* L. W. Taylor, ed.
    Fertility and hatchability of chicken and turkey eggs. Wiley, New York.
KEMPENAERS, B., F. ADRIAENSEN, A. J. VAN NOORDWIJK, AND A. A. DHONDT. 1996. Genetic
    similarity, inbreeding and hatching failure in Blue Tits: are unhatched eggs infertile?
    Proc. R. Soc. Lond. B 263:179–185.
———, B. CONGDON, P. BOAG, AND R. J. ROBERTSON. 1999. Extrapair paternity and egg
    hatchability in Tree Swallows: evidence for the genetic compatibility hypothesis? Behav.
    Ecol. 10:304–311.
KENDEIGH, S. C. 1942. Analysis of losses in the nesting of birds. J. Wildl. Manage. 6:19–26.
KOENIG, W. D. 1982. Ecological and social factors affecting hatchability of eggs. Auk 99:526–
    536.
———, J. HAYDOCK, AND M. T. STANBACK. 1998. Reproductive roles in the cooperatively
    breeding Acorn Woodpecker: incest avoidance versus reproductive competition. Am.
    Nat. 151:243–255.
LERNER, I. M. 1954. Genetic homeostasis. Wiley, New York.
MAYHEW, W. W. 1958. The biology of the Cliff Swallow in California. Condor 60:7–37.
MCRAE, S. B. 1996. Family values: costs and benefits of communal nesting in the Moorhen.
    Anim. Behav. 52:225–245.
MOSELEY, H. R., AND W. LANDAUER. 1949. Genetics and physiology of embryonic develop-
    ment. Pp. 244–337, *in* L. W. Taylor, ed. Fertility and hatchability of chicken and turkey
    eggs. Wiley, New York.
RALLS, K., P. H. HARVEY, AND A. M. LYLES. 1986. Inbreeding in natural populations of birds
    and mammals. Pp. 35–56, *in* M. E. Soule, ed. Conservation biology: the science of scarcity
    and diversity. Sinauer, Sunderlund, Massachusetts.
ROCKWELL, R. F., AND G. F. BARROWCLOUGH. 1987. Gene flow and the genetic structure of
    populations. Pp. 223–255, *in* F. Cooke and P. A. Buckley, eds. Avian genetics: a popula-
    tion and ecological approach. Academic, London, United Kingdom.
ROMANOFF, A. L. 1972. Pathogenesis of the avian embryo. Wiley, New York.
ROTHSTEIN, S. I. 1973. Variation in the incidence of hatching failure in the Cedar Waxwing
    and other species. Condor 75:164–169.
ROWLEY, I., E. RUSSELL, AND M. BROOKER. 1993. Inbreeding in birds. Pp. 304–328, *in* N. W.
    Thornhill, ed. The natural history of inbreeding and outbreeding: theoretical and em-
    pirical perspectives. University of Chicago Press, Chicago, Illinois.
SEEL, D. C. 1968. Clutch-size, incubation and hatching success in the House Sparrow and
    Tree Sparrow *Passer* spp. at Oxford. Ibis 110:270–282.
SIEGEL-CAUSEY, D., AND S. P. KHARITONOV. 1990. The evolution of coloniality. Pp. 285–330,
    in D. M. Power, ed. Current ornithology, vol. 7. Plenum, New York.
SITTMAN, K., B. ABPLANALP, AND R. A. FRASER. 1966. Inbreeding depression in Japanese Quail.
    Genetics 54:371–379.
STOCKLEY, P., J. B. SEARLE, D. W. MACDONALD, AND C. S. JONES. 1993. Female multiple mating
    behaviour in the common shrew as a strategy to reduce inbreeding. Proc. R. Soc. Lond.
    B 254:173–179.
VAN NOORDWIJK, A. J., AND W. SCHARLOO. 1981. Inbreeding in an island population of the
    Great Tit. Evolution 35:674–688.
WAGNER, R. H. 1993. The pursuit of extra-pair copulations by female birds: a new hypothesis
    of colony formation. J. Theor. Biol. 163:333–346.
WITTENBERGER, J. F., AND G. L. HUNT, JR. 1985. The adaptive significance of coloniality in

birds. Pp. 1–78, *in* D. S. Farner and J. R. King, eds. Avian biology, vol. 8. Academic, San Diego, California.

Zar, J. H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Upper Saddle River, New Jersey.