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EFFECT OF CLUTCH SIZE ON INCUBATION PERSISTENCE IN MALE WILSON'S PHALAROPES (*PHALAROPUS TRICOLOR*)

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ABSTRACT.—The effect of clutch size on incubation persistence of male Wilson's Phalaropes (*Phalaropus tricolor*) was studied over two breeding seasons in south-central Saskatchewan. The Wilson's Phalarope is a "sex-role-reversed" shorebird in which only males incubate and provide parental care. The breeding season is long enough to allow for renesting but not for the rearing of more than one brood per male. Barring secondary mating strategies, the total annual reproduction of a male is limited by the size of its clutch. Females lay determinate clutches of four eggs. By determining the minimum clutch size necessary for male incubation persistence, we demonstrated that males alter their reproductive effort in response to clutch size, and we identified the minimum potential annual reproduction for males necessary to maintain this unusual mating system. Clutch-size reductions led to an increased frequency of abandonment inversely proportional to the number of eggs remaining in the clutch. The timing of egg loss also was critical. Among males with clutches reduced to one egg or reduced to two eggs early in the incubation cycle, all but one abandoned incubation. Among males with clutches reduced to two eggs late in incubation or three eggs early, an intermediate proportion abandoned incubation. All but one male with three eggs late in incubation or a full, four-egg clutch continued to incubate. Experimentally increasing clutch sizes by two eggs over the normal four-egg clutch led to rapid nest failure. This suggests that the determinate, four-egg clutch of females is not suboptimal for males and that nest parasitism of two eggs by females has little potential benefit as an alternative reproductive tactic. *Received 24 February 1992, accepted 22 November 1992.*

THE MODERN study of clutch size began with Lack (1947a, b), who hypothesized that the number of eggs was limited by parental ability to provide for young. The idea applied particularly to altricial species provisioning nestlings with food. Lack also suggested that parental abilities could influence precocial species through less direct mechanisms (e.g. ability to brood chicks). Three central issues have been addressed in clutch-size investigations: (1) What are the evolutionary or ultimate factors that determine clutch size (reviews by Klomp 1970, Winkler and Walters 1983)? (2) What proximate factors affect clutch size, particularly direct environmental effects such as food and mineral availability, parental body condition (Klomp 1970, Winkler and Walters 1983), and physiological effects such as ovarian capabilities (Jones 1978)? (3) What is meant by determinate versus indeterminate clutches (Kennedy 1991)?

Given that clutch size represents the reproductive potential of a nesting effort, clutch size is likely to be critical in determining incubation tenacity. Nevertheless, the relationship of clutch size and persistent incubation in birds has received little attention. Hills (1980) added a fifth egg to six species of the Charadrii and found not only that fewer chicks hatched from supplemented clutches, but that all eggs hatched in only 6% of supplemented clutches versus 85% in nonsupplemented controls. An associated laboratory experiment, using Spotted Sandpipers (*Actitis macularia*) indicated an inability to incubate five eggs adequately. Kålås and Løfaldli (1987) felt that the three-egg clutch of the Eurasian Dotterel (*Charadrius morinellus*), a species in which only males incubate, was adaptive and allowed for high incubation constancy without an excessive energy demand on the male. This interpretation was based on the behavior of four males.

Absent from the literature are studies identifying minimal clutch sizes necessary for maintaining incubation. Klomp (1970), summarizing studies in which eggs are removed during the egg-laying stage to test for the determinacy of

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clutch size, stated, "one or two eggs are usually left to prevent desertion." Nolan (1978:174-175) associated nest abandonment by female Prairie Warblers (*Dendroica discolor*) with increased egg loss during the egg-laying stage. Optimal clutch size need not maximize annual reproductive success to maximize lifetime reproductive success (Charnov and Krebs 1974). Detailed information on the relationship of clutch size and incubation persistence is relevant to understanding reproductive effort in birds.

In birds, primary incubation of eggs by males is rare, occurring only within ratites, gruiforms, galliforms, cuculiforms, and charadriiforms (Oring 1982). However, male incubation provides an excellent opportunity to examine the relationship of clutch size to incubation persistence because the physiology of males is independent of egg laying. Only males incubate in the sex-role-reversed Wilson's Phalarope (*Phalaropus tricolor*). Wilson's Phalaropes breed at northern latitudes where a male can rear only one brood in a single breeding season. Barring secondary mating strategies, the total potential annual reproduction of a male is limited to the size of its clutch. We examined the incubation response of males to clutch sizes greater or fewer than four eggs.

Regardless of clutch size, male phalaropes likely incur costs associated with incubation that act to reduce fitness. For example, incubating males face the risk of predation at the nest, energy stress, and reduced opportunity for alternative reproductive behavior during the breeding season. As clutch size declines, potential fitness benefits decline making incubation behavior relatively more costly. Increased frequency of clutch abandonment with decreasing clutch size would indicate that males alter their reproductive effort in response to altered reproductive potential of the clutch. It is reasonable that there may be a lower limit to clutch size below which the costs of incubation exceed the potential fitness benefits. When incubation costs exceed the potential benefit, males may maximize their fitness by ceasing to incubate. Identifying such a lower limit is of special interest. Male incubation is intrinsic to the phalarope mating system. Thus, the minimum clutch size necessary for males to persist in incubation is a measure of the minimum potential annual reproduction necessary to maintain the mating system.

Examining the incubation response to artificially increased clutch sizes is relevant for two reasons. The determinate clutch size of females may be suboptimal for males. In shorebirds, exclusive male incubation is likely derived from an ancestral mating system that featured determinate clutch size and shared parental care (Jenni 1974). It has been argued that energetic constraints, including the demands of egg laying, might have contributed to female emancipation from incubation in several polyandrous shorebird species (Erckmann 1983). However, females in several sex-role-reversed species are known to be able to lay multiple clutches in rapid succession, although individual clutches are determinate (Hildén and Vuolanto 1972, Maxson and Oring 1980, Colwell and Oring 1988a). The ability of males to successfully incubate larger clutches, if it were found, would indicate that determinate laying by females may limit male fitness. Second, females compete intensively for access to males (Höhn 1969, Howe 1975, Colwell and Oring 1988b), with some females being prevented from pairing for at least part of the breeding season. Under these circumstances, one might expect unpaired females capable of laying eggs to engage in nest parasitism. Yet, this is extremely rare in Wilson's Phalaropes (Colwell and Oring 1988a, c). Experimentally increasing clutch size in this species simulates nest parasitism and provides an opportunity to observe the incubation responses of males faced with the presence of "parasitic" eggs.

Thus, altering clutch sizes in Wilson's Phalaropes allows us to address four objectives: (1) To examine the ability of male phalaropes to alter their reproductive effort in response to clutch-size changes. This is examined by measuring the frequency of clutch abandonment in relation to the timing and extent of clutch-size changes. (2) To identify the minimum clutch size necessary for males to persist in incubation, thus identifying the minimum potential annual reproduction for males necessary to maintain this unusual mating system. (3) To look for indications that, on an annual basis, the four-egg clutch of females is suboptimal for males. The ability of males to incubate enlarged clutches successfully would indicate that four eggs are potentially suboptimal. (4) To examine the viability of female nest parasitism as an alternative mating tactic by examining the response of incubating males to the introduction of two additional eggs.

METHODS

The breeding biology of Wilson's Phalarope has been studied extensively (Colwell 1986a, b, Reynolds et al. 1986, Colwell and Oring 1988a, b, c, d, e, Colwell et al. 1988). Females arrive on the breeding ground before most males. They compete intensively for access to breeding males by aggressively defending the area around males from other females. During the breeding season, egg laying by females appears to be constrained by access to males rather than by time or energetics. Females abandon the clutch, and the male, soon after clutch completion and compete for access to new males. Most females appear to get a mate during the breeding season, and some females are serially polyandrous. Females are able to lay multiple clutches in rapid succession. Clutch size is determinate at four eggs. Partial clutch loss is common, leaving clutches of one to three eggs ($\bar{x} = 3.8$).

Wilson's Phalarope eggs can hatch after 21 days of incubation (Höhn 1969), but incubation length is variable in the wild and averages 23 days (Colwell and Oring 1988a). Colwell and Oring (1988a) observed an average annual nest failure rate of 59%, with 21% of the failed nests having clutches that were abandoned by the incubating male. Four of 386 males (1%) were known to have been killed at the nest site.

Study site.—The study was conducted on two sites near the headwaters of Last Mountain Lake in south-central Saskatchewan: the Shields site (51°27′N, 105°10′W) in 1988 and 1989; and the Wreford site (51°24′N, 105°02′W) in 1989. Both consisted of wetland complexes within large, secluded, grazed grasslands. The 130-ha Shields site, a portion of the Lanagan Creek site used by Colwell and Oring (1988a), consisted of two creeks, one dammed to form a shallow reservoir, and several small, ephemeral wetlands surrounded by grasslands and patches of short woody vegetation. The Wreford site consisted of a large, irregular wetland fed by springs and two small streams, surrounded by pasture. Most observations at the Wreford site were made within an area of approximately 105 ha. The local flora and fauna have been described in detail (Colwell 1987, Dale 1987, Caldwell et al. 1987, Jorgenson 1987).

Monitoring of incubation.—In both 1988 and 1989, observations were made from early May through early July, spanning the period from before initiation of the earliest-known nests through hatch or failure of the last-known nests. Nests were checked frequently, at irregular intervals, throughout the incubation period, with most nests being checked at least once every two days. Typically, continued incubation was verified by observing the male flush from the nest. Clutch size was determined directly by peering into the nest cup. This usually did not require touching the nest, eggs, or surrounding vegetation. Time and disturbance at the nest site were minimized. Occasionally, flushing males were difficult to observe. In these cases, an egg was touched and warmth above ambient temperature was used to indicate recent incubation. Eggs were sometimes examined for the initial fractures indicative of impending hatch. This was done most often with clutches that were found after clutch completion.

Incubation persistence.—Nest abandonment was defined as intact eggs being left permanently unattended in an intact nest cup free of broken eggs, shell fragments, yolk, or albumin in or around the nest cup. In none of these cases did we see any indication that the incubating male had been injured or killed. Continued incubation was defined as incubation two or more days after clutch size changes occurred. In the case of males with unaltered clutch sizes, continued incubation was defined as incubation two or more days after entering the experiment. Most males that persisted incubating were captured at the nest as part of a separate endocrinological investigation (Delehanty 1991). Males that abandoned incubation within two days of being captured were assumed to have abandoned due to capture stress and were dropped from the analysis.

Treatments.—Nests found during egg laying were left undisturbed until clutch completion. Typically, four eggs were laid in four days. The day after clutch completion (day 2 of incubation), the male of each clutch was randomly assigned to one of several treatments.

In 1988, there were four treatments. (1) Males of nine nests were controls. Their clutches were not altered in any way. (2) Nine males had their clutches experimentally reduced to two eggs when we removed two randomly selected eggs from the full clutch. Males of the first five clutches to receive this treatment, performed on day 2 of incubation, immediately abandoned the remaining two-egg clutches. For the remaining four males, we removed two viable eggs from the clutch and replaced them with two surrogate eggs. Surrogate eggs consisted of Wilson's Phalarope eggs collected from abandoned clutches and parboiled. On approximately day 12, the clutch was reduced to the two original eggs. (3) Nine males had their clutches supplemented by two eggs on the second day of incubation. Using the viable eggs from the reduced-clutch nests, we inserted two eggs into random positions within the four-egg clutches. Introduced eggs were of equal age to the original four eggs of supplemented clutches and all eggs were viable. (4) To distinguish male incubation response to increased clutch size from response to the presence of introduced eggs, 10 males were assigned to a "cross-clutch" treatment. For these males, two of their four eggs were switched with two eggs of equal age from the nest of another cross-clutch male. Thus, males with cross clutches had viable, four-egg clutches consisting of two original eggs and two introduced eggs.

In 1989, six males were controls, and six males had reduced clutches. We removed only one egg from males in 1989, however, and did so on day 2 of incubation. This imitated natural egg attrition observed in 1988. Eight males had clutches that were supplemented to six eggs. Because fewer nests were available in 1989, some supplemented clutches received one or two surrogate eggs. No males had cross clutches in 1989.

In both 1988 and 1989, natural egg attrition was frequently observed. Single-egg losses were most common. We suspect much of this egg loss was caused by mice.

After 14 June 1989, nests found with complete, four-egg clutches were randomly assigned to treatments of a second clutch-size experiment, the "midincubation experiment." We increased 10 four-egg clutches to six eggs during midincubation by adding two surrogate eggs. Nine nests were designated as controls, and these clutches were left unaltered. Excluding the clutches supplemented for the midincubation experiment, clutches found after clutch completion were not altered. Clutches never observed to include four eggs were not altered.

Statistical analysis.—Male response to reduced clutch size was analyzed by excluding all males with supplemented clutches, then pooling all males with similar clutch sizes. The full-clutch group consisted solely of males with four eggs for which the clutch was monitored from egg laying through the termination of incubation (i.e. primarily the pool of males with four eggs from control and cross-clutch nests). Males with fewer than four eggs consisted of males with experimentally reduced clutches, and males that experienced partial clutch losses during incubation.

Because some nests were found after clutch completion and ultimately failed, the precise day of incubation at which clutch loss occurred could not always be determined. However, the timing of most losses could be distinguished as early incubation (through day 7) versus late incubation (day 8 to hatch). In cases where an incubating male experienced a partial clutch loss, the incubation response to the new clutch size was treated as an independent measure of response to clutch reduction.

The frequency of abandonment versus continued incubation was compared using the conditional binomial exact test, case 1 (Rice 1988). This is an exact test that accommodates low sample sizes ($n < 6$). Expected frequencies are derived from the sample data, avoiding *a priori* assumptions about expected frequencies. For clutch-size reductions we hypothesized that incubation persistence would be promoted by larger clutch sizes and advancement through incubation. Therefore, pairwise tests are one-tailed. The sequential Bonferroni technique was used to evaluate the experimentwise ("tablewide") significance level for each pairwise comparison when *a posteriori* multiple comparisons were performed (Rice 1989). Where multiple comparisons are made, only the experimentwise probability for each pairwise comparison (P_{exp}) is reported.

RESULTS

Clutch-size reductions.—Males were highly sensitive to clutch-size reductions. Males with reduced clutches ($n = 50$) abandoned incubation with significantly greater frequency than full-clutch males ($n = 31$, $P < 0.001$). The frequency of continued incubation depended on the number of eggs remaining in the clutch. Males did not abandon three-egg clutches ($n = 28$) with significantly greater frequency than males with full, four-egg clutches ($P_{exp} = 0.171$), although the individual pairwise probability ($P = 0.089$) was suggestive of a difference. One male abandoned a four-egg clutch; four males abandoned three-egg clutches. However, males with clutches of two or one egg ($n = 17$ and 5, respectively) did abandon with greater frequency than full-clutch males (four eggs vs. two, $P_{exp} = 0.029$; four eggs vs. one, $P_{exp} < 0.001$). Males with one-egg or two-egg clutches also abandoned incubation with greater frequency than males with three eggs (three eggs vs. two, $P_{exp} < 0.001$; three eggs vs. one, $P_{exp} < 0.001$). Abandonment frequency did not differ between males with two-egg and one-egg clutches ($P_{exp} = 0.171$) although, here too, the individual pairwise probability ($P = 0.091$) was suggestive of a difference. Twelve of 17 males with two eggs abandoned their clutches as did all five males with one-egg clutches.

The timing of egg loss relative to the incubation cycle also was critical. This was revealed by comparing abandonment rates among males for which the stage in the incubation cycle at the time of clutch reduction was known (Fig. 1). Among males with full clutches or three-egg clutches late in incubation (group C), only one case of clutch abandonment was observed. Among males with clutches reduced to one egg or to two eggs early in incubation (group A), only one case of continued incubation was observed. Males with two eggs late in incubation or three eggs early in incubation (group B) abandoned incubation at an intermediate frequency relative to groups A and C. Our *a posteriori* pairwise comparisons of groups A, B, and C indicated that abandonment frequency differed significantly between groups (A vs. B, $P_{exp} > 0.001$; A vs. C, $P_{exp} < 0.001$; B vs. C, $P_{exp} = 0.001$). Abandonment frequencies did not differ within groups A, B, or C (full clutch vs. three eggs late, $P = 0.775$; three eggs early vs. two eggs late, $P = 0.223$; two eggs early vs. one egg, $P = 0.356$). Thus, stage in the incubation cycle when partial clutch loss occurred, as well as size of the remaining clutch, affected abandonment frequency.

Clutch-size increases.—Supplementing full clutches with two additional eggs had a rapid, negative effect on nest success. Fourteen of 17 supplemented clutches failed during early incubation, including those of two males that abandoned immediately. These nests failed before or shortly after capture of incubating males ($n = 6$ and 8, respectively). Eight nests also suffered partial clutch losses during this time. The occurrences of partial clutch loss and postcapture abandonment were effects of clutch size per se, rather than effects due to the presence of introduced eggs. Males with supplemented clutches had significantly higher rates of both partial clutch loss and postcapture abandonment than cross-clutch males ($P = 0.001$ and 0.002, respectively). Similarly, males with supplemented clutches experienced higher rates of partial clutch loss and postcapture abandonment than the pool of all males with four or fewer eggs ($P = 0.001$ and 0.006, respectively). Finally, all cross-clutch males incubated their four-egg clutches, despite the presence of two introduced eggs. Thus, greater clutch size, rather than the presence of introduced eggs, led to rapid nest failure for males with supplemented clutches.

These results were corroborated by the additional clutch-supplementing experiment of 1989 (the midincubation experiment). Ten active nests with four-egg clutches received two additional eggs during midincubation. Seven of these nests failed within four days of the treatment ($\bar{x} = 3.14 \pm$ SD of 0.69). Only two of nine control nests failed in this same time period. The failure rate within four days after treatment was significantly greater for nests with supplemented clutches than for controls ($P = 0.020$). Again, partial clutch loss was pervasive for supplemented clutches, with 5 of 10 nests incurring partial clutch loss near the time of nest failure. Only two males still retained six eggs when they abandoned incubation. The greater frequency of partial clutch loss in this period for supplemented clutches (5 of 10) compared to controls (1 of 9) also was significant ($P = 0.037$).

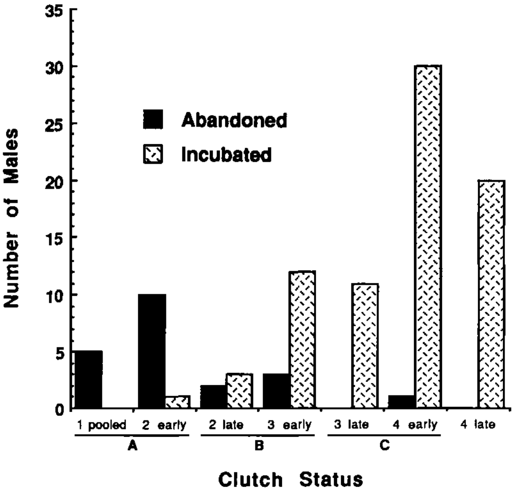

Fig. 1. Occurrence of clutch abandonment or continued incubation by male Wilson's Phalaropes relative to clutch status. Clutch status refers to number of eggs in clutch (1–4) and when, during incubation cycle, any clutch-size reduction occurred (early, through day 7 of incubation; late, day 8 to hatch; or early and late pooled in the case of males with one-egg clutches). A, B, and C indicate groups of males compared via *a posteriori* tests in the text. Males with four-egg clutches that persisted through early incubation make up the "4 late" clutch status.

Of three males with supplemented clutches that continued incubation, one suffered partial clutch loss and failed, one had the nest cup disturbed by cattle and abandoned the clutch, and one hatched four chicks. In the latter two nests, however, the surrogate eggs were removed after the male was captured and, thus, the incubating male was subjected to six eggs for less than one week.

DISCUSSION

Male incubation persistence.—The timing and extent of partial clutch loss was critical to continued incubation in male Wilson's Phalaropes. The frequency of abandonment increased progressively as clutch size decreased, particularly if reduction occurred in early incubation. To engage in incubation, Wilson's Phalarope males required a clutch size of two, provided that the total incubation period and, thus, the full costs of incubation did not lie ahead. If the full incubation period remained, males required a clutch of three eggs.

This interpretation is based on the following points. Clutch abandonment by males with full clutches or three-egg clutches in late incubation was very rare. Males incubated with great persistence for a potential annual reproduction of four, or three if the full incubation period did not lie ahead. Compared to the group of males with full clutches or three eggs late in incubation, the frequency of abandonment increased significantly for the group of males with three-egg clutches in early incubation or two-egg clutches in late incubation. Still, many males with clutches at these sizes and stages continued to incubate. The potential fitness benefits might have been close to the costs of incubation, and it was difficult to predict the behavioral response of a given male under these circumstances. Finally, continued incubation was very rare for males with two-egg clutches in early incubation, while no males persisted in incubation with one egg. In these situations, the costs of incubation probably exceeded potential fitness benefits.

A potential physiological mechanism mediating this flexible incubation behavior has been identified. Prolactin (*Prl*) has long been associated with incubation in birds (reviewed by Goldsmith 1983, 1991, Buntin 1986, Lea 1987). Male incubation in several shorebird species, including the Wilson's Phalarope, is strongly linked to elevated *Prl* (Oring et al. 1986a, b, Oring et al. 1988, Fivizzani et al. 1990, Gratto-Trevor et al. 1990, Oring and Fivizzani 1991). In one year of this study, males that continued to incubate two-egg and three-egg clutches had significantly lower levels of circulating *Prl* than males with clutches of four eggs (Delehanty 1991).

The measure of minimum clutch size, or minimum potential annual reproduction, necessary for male Wilson's Phalaropes to persist in incubation is valuable provided that it is viewed in terms of the prevailing environmental and social conditions. During the first year of our study, weather conditions were unusually harsh. It is difficult to predict how this might influence incubation persistence after partial clutch loss. While identifying a minimum clutch size for male incubation gives insight into maintenance of a sex-role-reversed mating system, it does not necessarily measure selection forces that gave rise to it.

Are four-egg clutches suboptimal?—We found no evidence that four-egg clutches are suboptimal for males. Supplementing clutches with two additional eggs led to nest failure. At least once in each supplemented nest, the male rearranged the eggs into a compact configuration that appeared to minimize the total exposed surface area of the eggs. We interpreted this to mean that all males with supplemented clutches, even those that quickly abandoned, attempted to incubate the six-egg clutch.

The failure of males to incubate six-egg clutches successfully was strongly linked to clutch size rather than presence of introduced eggs. Like supplemented clutches, cross clutches contained two introduced eggs, although the total clutch size of cross clutches was four. Males with cross clutches incubated with great persistence, while those with supplemented clutches failed.

Further evidence that male phalaropes do not recognize individual eggs, but can respond to clutch-size changes, is found by comparing the incubation response of males with cross clutches in early incubation to males with clutches reduced to two eggs in early incubation. Cross clutches and clutches reduced to two eggs in early incubation represent a total fitness potential of two young to the incubating male. Yet, all cross-clutch males, with their total clutch size of four, persisted incubating, while all but one of the males with two eggs abandoned their clutch.

Potential for female nest parasitism.—A striking feature of supplemented clutches was the high incidence of partial clutch loss. We do not know the causes of egg attrition in these clutches. It might have been that males with supplemented clutches had reduced nest attendance compared to males with full clutches and, for that reason, their clutches were more susceptible to predators (e.g. mice) that often take just one egg (Maxson and Oring 1978). We felt that reduced attendance was likely, based on our impression that males with supplemented clutches were absent from the nest more often than males with full clutches. Also, the nest cup seemed untidy, and the eggs dusty and unpolished in the nests of some males with supplemented clutches, unlike those of most full-clutch males. Males with supplemented clutches seemed to require more time to return to their nests during efforts to capture them.

The greater rate of postcapture abandonment by males with supplemented clutches compared with those having full clutches and cross clutches suggests that the additional eggs were stressful in some way. Capture and handling of males undoubtedly causes some stress, although normally not enough to lead to abandonment in males with full clutches. Since males with supplemented clutches abandoned after capture significantly more often than males with full and cross clutches, it appears that additional eggs, combined with capture stress, led to abandonment.

Another plausible explanation for failure of nests with supplemented clutches is that the clutch did not provide the correct stimulatory cues for continued incubation. Despite various intricate arrangements of six eggs by males, the exposed area of the eggs appeared to exceed the surface area of the paired incubation patches found on incubating males. Typically, the four eggs of a full clutch are arranged symmetrically in a way that allows two eggs to be in contact with each incubation patch. Six eggs necessarily had a greater surface area, and most arrangements were asymmetrical.

Hills (1980) found asymmetry and uneven heating of the entire clutch for an experimentally supplemented five-egg Spotted Sandpiper clutch, and suggested that an individual egg may be in a cold position long enough to kill the embryo. Andersson (1978) felt that size of the incubation patch in shorebirds limited the total egg volume that could be incubated. Perhaps males simply could not maintain proper incubation temperatures sufficiently in a supplemented clutch. The sole successful male with a supplemented clutch hatched only three of the six eggs and required four days of incubation beyond the mean incubation period of successful nests in that year.

Increased nest failure in nests with additional eggs would act to limit the reproductive success of parasitic females. In this sense, and assuming that rearing parasitic chicks is costly, a propensity for males to abandon clutches with two extra eggs or to reduce nest attendance at such nests may be adaptive and may help explain the upper clutch-size limit of four.

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