$P < 0.001$), and the greater number of helpers in groups with related helpers may have resulted in one helper responding more quickly than in the other groups; all test groups had helpers. We have no information on the cost of mobbing; none of the three naturally occurring mobbings of cuckoos that we observed in the field involved a counter-attack by the cuckoo.

Although we traditionally describe a helper's aid as that which is given to the breeding relative (Hamilton 1964), in most cases we could just as well describe its offspring as the recipient, as is stressed in the close relationship between workers and diploid offspring in the haplodiploid eusocial Hymenoptera. Helper feeding in birds and bees is directed mainly toward the young, not the breeders. In cooperative birds it seems appropriate to consider kinship between helpers and adult breeders as the kinship involved in the evolution of helping behaviour, rather than kinship between helpers and offspring, because the young that are aided are not necessarily related to the breeders or the helpers, though usually they are. The young in splendid fairy-wren nests are often parasitic cuckoos *C. basalis* (Rowley 1981). In the splendid fairy-wrens, helpers defended both nests with young wrens and nests with young cuckoos (no nests had both cuckoos and young wrens, because cuckoos hatch first and evict the wren eggs, but two nests with hatchling cuckoos still had wren eggs and we count these as nests with cuckoos). In the tests, 27 of 40 helpers responded in defence of wren eggs or young in the nest, and 13 of 16 helpers responded in defence of a cuckoo nestling (Fisher exact test, $P = 0.16$, NS). The mean time from discovery to mobbing for responding helpers was shorter when a young cuckoo was in the nest (mean $\pm$ SD of 13 helpers with a cuckoo nestling $= 8.23$ s ± 9.00, mean $\pm$ SD of 27 helpers with no cuckoo $= 16.52$ s ± 24.26; Mann–Whitney U-test, $z = 5.20$, $P < 0.001$), contrary to behaviour expected by kinship of helper and young; all helpers were closely related ($r \geq 0.5$) to at least one breeding fairy-wren in their group.

The results suggest that the incidence and latency of nest defence by non-breeding fairy-wrens is not proximally determined by kinship. In general, the helpers in these cooperative groups defend the nest regardless of variations in their kinship with the breeding adult wrens and the young in the nest.

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Parental Investment Based on Clutch Value: Nest Desertion in Response to Partial Clutch Loss in Dabbling Ducks

Parents should invest in current young only to the extent that doing so balances the value of current offspring with the chance of producing more offspring in the future. However, empirical studies designed to test predictions from parental investment theory have not provided a clear indication as to whether parental investment is based on previous reproductive investment or on expected benefits from the breeding attempt (e.g. Robertson & Biermann 1979; Weatherhead 1979, 1982; Dawkins & Brockmann 1980; Biermann & Robertson 1981; Carlisle 1985).

Offspring abandonment has been reported in a variety of vertebrates (Kynard 1978; Zwickel & Carveth 1978; Tait 1980) but has not been used to examine parental investment theory. Nest predation, nest parasitism and small brood sizes all lower the value of the current reproductive event and may cause parents to abandon their offspring (Hamilton & Orians 1965; Tait 1980).

This study examined nest desertion by female blue-winged teal, *Anas discors*, and northern shoveler, *A. clypeata*, in response to experimental reductions in clutch size to test the hypothesis that parents invest in clutches based on expected benefits rather than on past investment. Nest desertion should be an unambiguous way to test parental investment theory because parents derive no benefits from a deserted nest and have limited future options: to re-nest with the opportunity to raise a larger brood or to forego reproduction (and save reproductive effort) until the next breeding season. The fitness gains from abandoning a clutch are unknown, but there should be no systematic bias caused by differences in these benefits if birds are randomly assigned to treatments. However, the benefits of continued investment are greater for a large clutch than a small one in dabbling ducks, *Anas* spp. (Rohwer 1985). The hypothesis of expected benefits predicts that the frequency of nest desertion would be inversely related to experimental clutch size, whereas the past investment hypothesis predicts that there will be no relation between final clutch size and the frequency of nest desertion. We limit our discussion to the maximization of the benefits of parental investment trade-offs (rather than net benefits) because the costs (energetic and risk of predation) of incubating clutches of different sizes are unknown.

The study was conducted from May to July 1985 within the aspen parkland region of southwestern Manitoba, Canada, approximately 10 km southeast of Minnedosa, (50°10′N, 99°45′W). We located teal and shoveler nests by flushing females from their nests.

Sixty-eight blue-winged teal nests were assigned randomly to one of three treatments and were manipulated 17 days after the first egg was laid. Experimental clutches were reduced to either four or seven eggs, while control nests were disturbed in a similar manner, but clutch size was not changed from the normal 10.6 ± 0.12 eggs ($\bar{X} \pm \text{SE}$, $N=68$). Fourteen northern shoveler nests were assigned to either the control or the four-egg treatment and were manipulated 18 days post-initiation. The normal shoveler clutch size was 10.3 ± 0.32 eggs ($\bar{X} \pm \text{SE}$, $N=14$).

Clutch initiation dates were determined by back-dating with the assumption that teal and shoveler lay one egg per day and commence incubation on the day the last egg is laid (Bellrose 1980). Stage of incubation was determined using a field candler (Weller 1956).

Nests were visited daily after manipulation to determine whether the female had abandoned the clutch, except when wind speeds exceeded 35 km per h or during rain. At every nest check the eggs were counted and covered with nest material as they would have been by a duck leaving the nest on an incubation recess. Nests were considered abandoned if they were left unincubated for 2 consecutive nights.

Blue-winged teal abandoned reduced clutches more often than those from which eggs had not been removed. Desertion rates were: 85%, 17% and 0% for clutches reduced to four eggs ($N=27$), seven eggs ($N=18$) and the controls ($N=23$), respectively (seven eggs versus control $P<0.025$, all other comparisons $P<0.001$). Northern shovelers deserted 50% of the four-egg clutches ($N=6$), but none of the control nests ($N=8$, $P<0.025$). Abandonment occurred within 24 h of the clutch manipulation. Teal did not abandon any nests until clutch reduction exceeded 30%, but all nests from which more than 65% of the eggs had been removed were abandoned (Fig. 1). The percentage of reduction in clutch size was a good
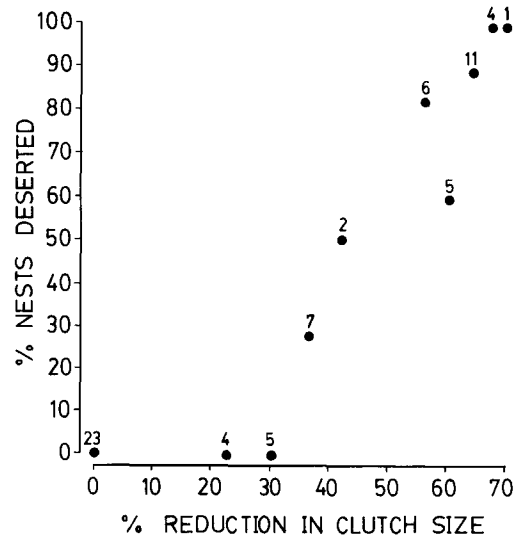

Figure 1. Weighted regression of the percentage of nests deserted by blue-winged teal, *Anas discors*, on the percentage of the clutch that was removed. Weighted regression was performed on angular-transformed percentages. Numbers indicate sample sizes. Twenty-three control nests (0% clutch reduction) were omitted from the analysis. $r^2 = 0.91$, $N=45$.

predictor of nest desertion in teal ($r^2 = 0.91$, regression on angular-transformed data weighted by sample size, Fig. 1). Control nests were excluded from the regression analysis because clutch size had not been altered in these nests. Females that abandoned their nests did not differ from females in the same treatment that continued incubation in the timing of egg laying or incubation, nor initial clutch size (one-way ANOVAs, all $Ps > 0.05$).

Blue-winged teal and northern shovelers did not base abandonment decisions on some measure of past investment, such as the number of eggs laid or the length of time spent investing in the nest, but appeared to continue to assess the costs and benefits of alternative parental investment tactics during incubation as predicted by parental investment theory (Carlisle 1982). If initial clutch size is an accurate measure of past parental investment then the past investment hypothesis can be rejected. Whether the females used the decrement in clutch size or the number of eggs remaining in the nest as the basis for future investment decisions is not clear, but the two mechanisms would produce similar results.

Nest abandonment was not simply a result of disturbance by potential predators as Hamilton & Orians (1965) suggested, because no control nests were abandoned in spite of being disturbed repeatedly. Nor was nest desertion a simple response to partial clutch loss because teal deserted four-egg nests more often than seven-egg clutches. The probability of the female being killed by a predator that had previously removed part of her clutch would be independent of the number of eggs removed from or left in the nest.

Current clutch size or the number of eggs lost are good predictors of the value of a nest and strongly influenced nest desertion by blue-winged teal and northern shoveler. Nest initiation date and initial clutch size, which may be related to a duck's ability to produce a replacement clutch, may also influence parental investment decisions but neither was a significant factor in this study. Therefore, blue-winged teal and northern shoveler appear to make parental investment decisions based on the value of the current nest (which is equivalent to the expected benefits from the clutch) and are not restricted to assessing the utility of future investment by the amount of effort already committed to a breeding attempt.

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