

the adult plumage is likely retained unchanged for the life of the individual. The biological significance of this highly variable adult female plumage is unknown but may be unique among passerines. The possibility exists that highly melanistic females select more male-like habitat in the nonbreeding season (habitats described in Lynch et al. 1985). In this case, the melanism might function as a threat and be displayed in aggressive situations, as is the case with males (Rappole and Warner 1980). However, more recent studies of territorial female Hooded Warblers in Mexico indicate that males and females prefer different habitat in the nonbreeding season and do not compete with each other for territories. Moreover, females exhibiting all plumage classes were seen in the same habitat (Morton et al. 1987). Furthermore, we found no evidence that subadult female plumage or degree of melanism exhibited by individual adult females was related to winter territory habitat quality, although this possibility needs further testing. The existence of both a distinctive subadult female plumage, a rarity among passerine birds (Stutchbury and Robertson 1987), and a highly variable adult female plumage, suggests that more study of the Hooded Warbler is warranted throughout its annual cycle.

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The impact of male parental care on female Eastern Kingbird reproductive success.—Male parental care generally is assumed to improve survival of nestlings and increase female reproductive success (fitness). Consequently, the need for male assistance is considered by some to be responsible for the evolution of monogamy when the investment of the male is

not shareable among mates (Wittenberger and Tilson 1980). However, Gowaty (1983) found that reproductive success was not different between lone and paired female Eastern Bluebirds (*Sialia sialis*) and argued that monogamy is not necessarily maintained only by the need for male care. Bart and Tornes (1989) cite several examples of male-removal studies that indicate the presence of a male is of little value in many species, but they conclude that apparent care by the male does tend to benefit the young.

In this study we attempted to determine the impact of male parental care on female reproductive success in the monogamous Eastern Kingbird (*Tyrannus tyrannus*). Male Eastern Kingbirds help to feed, guard, and defend their young throughout the breeding cycle. Males also aid in the 3- to 4-week period of post-fledging care (Morehouse and Brewer 1968).

Methods.—This study was conducted at Eastern Kingbird nests on and around Lake Opinicon, Ontario, from May to August 1986. The study site is described in detail by Blancher and Robertson (1985). Five resident males were removed experimentally by shooting when the nestlings were one day old. Shooting (Canadian Wildlife Service Permit #EK290) was necessary because we did not know of any way to keep these aerial insectivores alive in captivity for the necessary time period. For this reason a very small sample size was used. Seven nests that corresponded in nesting time and habitat to the experimental nests were chosen at the time of the removals and were used as unmanipulated controls. We measured feeding rates per nestling by watching nests for 60 min intervals every other day during the nestling period. These observations were carried out at approximately the same time each day. Nests were watched from a distance of approximately 30 m to avoid disturbing the birds. Following each watch, nestlings were weighed with a Pesola spring balance, and each nestling's 9th primary was measured to the nearest mm. We also quantified nest defense at each nest four times during the nesting cycle (incubation days 1–6, 7–14; and nestling days 1–4, 5–8) by scoring the aggressiveness of the birds during a 5-min trial to a simulated predator (plastic crow) placed approximately 1 m from the nest. Responses were scored on a scale of 0 to 5 (0—no response; 1—silent observation; 2—vocalization and hovering; 3—few single dives; 4—continuous diving; 5—striking the crow). Repeat testings on nests were carried out with a minimum of four days between presentations in an effort to avoid habituation. Males and females were distinguished by their behavior (for example, favorite perch locations) and by noting which bird was at the nest. In nesting pairs, one of the birds is almost always guarding the nest, resulting presumably in fewer losses to predators. Smith (1966) noted this trade-off pattern, and found that the male was present 82% of the time when the female left the nest and 91% of the time when she returned. Predation was assumed if the entire brood disappeared at one time with no evidence of poor weather or dead nestlings.

Results.—Following removal of resident males, potential replacement males were seen at all five experimental nests. In two cases, the resident female was aggressive and the intruders did not persist. In two other cases, the intruders likely were neighboring males which occasionally were accompanied by a third bird, presumably a mate. In the fifth case, a replacement male arrived on the day of the removal and persisted until the nestlings fledged. This male defended the territory but was indifferent toward the nestlings (failure to feed and/or harass). Broods at all five experimental nests were raised by the female alone, since the only persistent male did not feed the nestling.

There was no significant difference between the clutch sizes of unassisted ($\bar{x}_1 = 3.4 \pm 0.49$ [SD]) and assisted groups ($\bar{x}_2 = 3.5 \pm 0.50$; Mann-Whitney U-test, $N_1 = 5$ $N_2 = 7$, $U = 14.5$, $P > 0.30$). The brood size at hatching also indicated no significant difference between the unassisted ($\bar{x}_1 = 2.60 \pm 0.49$) and assisted groups ($\bar{x}_2 = 2.85 \pm 0.64$; Mann-Whitney U-test, $N_1 = 5$ $N_2 = 7$, $U = 14$, $P > 0.30$) (Conover 1980).

A significant difference did exist between the survival of the nestlings in broods raised by unassisted females and those having biparental care. None of the five unassisted females managed to fledge her entire brood, however, in 57% (4/7) of the broods attended by two parents, all nestlings survived to fledge (G -test, $G_{\text{adj}} = 4.96$, $P < 0.03$).

The entire brood was lost to predators in 60% (3/5) of the nests attended by unassisted females, but only 29% (2/7) of the nests of assisted females were depredated (G -test, $G_{\text{adj}} = 1.05$, $P > 0.30$). Unassisted females also suffered greater partial brood loss than did assisted females. Of the seven nestlings that escaped predation in nests of unassisted females, four died (57.1%), apparently due to starvation (based on mass, size, and appearance of the nestlings). However, only 7.7% (1/13) of the nestlings that escaped predation in nests of assisted females died prior to fledging (G -test, $G_{\text{adj}} = 5.24$, $P < 0.02$). As a result of both predation and partial brood loss, only 23% (3/13) of the nestlings which hatched in unassisted females' nests eventually fledged, whereas 60% (12/20) of the nestlings that hatched in the nests of assisted females survived to fledge successfully (G -test, $G_{\text{adj}} = 2.04$, $P > 0.10$).

Although there were differences in survivorship between nestlings in assisted and unassisted nests, there was no significant difference in either mean nestling weight or mean 9th primary length between the two groups (Table 1). The growth of the surviving nestlings was apparently kept at a normal level by unassisted females through partial brood loss. That growth was normal in surviving young in both groups is indicated by the same ages at fledging for nestlings in assisted and unassisted nests (17 days).

A repeated measures analysis of variance was used to determine whether feeding rate (deliveries/nestling/hour) was affected by the presence or absence of a male care-giver (treatment) and/or the age of the nestlings (stage). It was found that unassisted females fed at a higher rate ($\bar{x} = 1.25 \pm 0.37$) than did assisted females ($\bar{x} = 0.99 \pm 0.26$; $F_{1,57} = 5.49$, $P < 0.03$), indicating an attempt to compensate for the loss of a mate. Neither stage ($F_{2,55} = 1.09$, $P > 0.30$) nor the interaction treatment $\times$ stage ($F_{2,55} = 0.56$, $P > 0.55$) significantly affected feeding rate. The latter does not, however, correspond with Morehouse and Brewer (1968) and Murphy (1983) who found feeding rates to be affected by stage.

There was no significant difference between the feeding rates of the unassisted female and the combined feeding rates of the control males and females ($F_{1,57} = 0.06$, $P > 0.80$). Unassisted females thus achieved the same feeding rates per nestling per hour as the control pairs; however, this was possible only because of both partial brood loss and an apparent reduction of time spent brooding and nest guarding. It is also possible that they increased their rates by substituting quantity for quality of prey type, since the food quality of the females was not determined. Replications of the ANOVA tests using ranked data indicate that our results were valid and not artifacts of non-normal distributions (Conover 1980).

Prior to removing the males, nest defense aggression scores for unassisted and assisted females were similar (unassisted: $\bar{x}_1 = 1.33 \pm 0.94$; assisted: $\bar{x}_2 = 1.43 \pm 0.78$; Mann-Whitney U -test, $N_1 = 3$, $N_2 = 7$, $U = 8$, $P > 0.30$), and although not significant, the males tended to vocalize, hover near the nest, and dive and strike at the simulated predator more often and more aggressively ($\bar{x}_1 = 2.00 \pm 1.41$) than did the females ($\bar{x}_2 = 1.43 \pm 0.78$; Mann-Whitney U -test, $N_1 = 7$, $N_2 = 8$, $U = 17$, $P > 0.10$). Once their mates were removed, a change was noted in the unassisted females; they became significantly more likely to dive at and strike the crow ($\bar{x}_1 = 4.25 \pm 0.75$) than their paired female counterparts who seldom struck the model ($\bar{x}_2 = 2.67 \pm 1.67$; Mann-Whitney U -test, $N_1 = 3$, $N_2 = 7$, $U = 0$, $P < 0.01$). Unassisted females thus increased their aggressiveness toward the predator once they lost their mates. In general, the unassisted females seemed to take on a behavioral role midway between that of the control males and females. They chased away predators and guarded the nest more aggressively than the control females did, but they appeared unable to reach the level of defense achieved by the control pair combined.

TABLE 1
MEAN NESTLING WEIGHT AND MEAN 9TH PRIMARY LENGTH ON DAY 11 (LAST DAY OF MEASUREMENTS PRIOR TO FLEDGING) FOR UNASSISTED AND ASSISTED FEMALES

	Assisted females	Unassisted females	<i>t</i> ^a	<i>P</i>
Number of nestlings	12	3		
Mean nestling mass (g)	34.46 ± 2.96	32.67 ± 0.85	1.04	>0.10 ns ^b
Mean 9th primary length (mm)	26.08 ± 2.25	23.33 ± 1.25	2.04	>0.05 ns

^a *t* = Student's *t*-test.

^b ns = not significant.

Discussion.—In kingbirds it appears that although some females can successfully fledge some young on their own, nesting success is reduced in the absence of male parental care. Although not essential, male help plays a very important role in raising young. Decreased survival rate of nestlings of unassisted females was caused both by increased predation and increased single nestling deaths. Increased predation is likely a result of decreased time spent on nest guarding and defense, since a parent was no longer almost constantly at the nest. Blancher and Robertson (1982) found that kingbirds are capable of successfully deterring predation by their aggressive behavior.

The increase in the number of single nestling deaths in nests of unassisted females appeared to occur due to starvation and/or increased exposure to adverse weather conditions. This increase in the death rate indicates that males play an important role in feeding nestlings and allowing the female to brood the young. This care is probably most important in years of poor weather. Beissinger (1986) found a decrease in nesting success during bad weather in Snail Kites (*Rostrhamus sociabilis*) and proposed that postfledging success declined in drought years concluding that during favorable weather one bird could successfully raise the brood. Bart and Tornes (1989) also found that parental care by male House Wrens (*Troglodytes aedon*) benefited the nestlings only in unfavorable periods.

Environmental conditions may also affect parental responses such as the allocation of male reproductive effort. For example, increased polygyny could result if weather conditions are favorable (Beissinger 1986). This could be a partial explanation for the apparent attempts of the two neighboring males to acquire an additional mate, and their subsequent failure to do so. That is, the weather in the spring and summer of 1986 was wetter and cooler than normal: June 1986, average temperature = 15.6°C (normal = 16.7), total precipitation = 131.6 mm (normal = 64 mm); July 1986, average temperature = 19.6°C (normal = 20.1), total precipitation = 74.6 mm (normal = 53.2 mm) (Environment Canada Climate Service, pers. comm.).

Murphy (1983) found that unpredictable changes in temperature and precipitation dramatically affect the ability of adult Eastern Kingbirds to feed young. The main diet of flying insects decreases in cool and wet weather. He found that most nestlings that died of starvation did so during cold, rainy periods. It follows that the impact of weather could have important implications for the present study since the summer of 1986 was cooler and wetter than normal. If data collection had been during favorable feeding conditions, female reproductive success might have been greater, possibly indicating that male parental care is necessary only during unfavorable conditions.

Although some nestlings raised by unassisted females survived to fledge, whether or not they survived the 3- to 4-week period of post-fledging care is not known. It is possible that

they did not survive this period, since Morehouse and Brewer (1968) report that this is the time of maximum parental care and energy requirements of the young.

The unassisted females' attempts to compensate for the loss of their mates resulted in their increasing the number of feeding trips over the breeding cycle, and increasing aggressiveness in nest defense. The experimental nest with the largest nestlings best demonstrates the need for male help. Here, the replacement male was indifferent to the nest, but did help the female defend the territory. The time required for nest defense by the female probably was reduced, allowing her to brood and feed the nestlings more successfully. These nestlings were slightly larger on Day 5 (chosen since there were still a total of 9 nestlings alive) than were those of experimental nests without a defending male (however, the difference was not statistically significant).

Our results are consistent with aspects of other studies of the significance of male parental care to female reproductive success. Hannon (1984) reported an increase in predation with the loss of male Willow Ptarmigan (*Lagopus lagopus*), indicating that male vigilance in other species also plays an important role in nest defense. Lyon et al. (1987) found widowed female Snow Buntings (*Plectrophenax nivalis*) increased their feeding rates in an attempt to make up for the loss of their mates. Despite this compensation by the females, they suffered reduced reproductive success compared with assisted females. Similarly, Leffelaar and Robertson (1986) found that female Tree Swallows (*Tachycineta bicolor*) could compensate for a mate's absence for a short period of time, but lone females were less successful in rearing young than paired females.

In addition to the possible necessity of male parental care (Wittenberger and Tilson 1980), Freed (1987) proposed that males may be constrained to monogamy for various reasons. For Eastern Kingbirds these constraints could include a limited number of females, female aggression, short breeding season, and variable weather conditions. Whether the evolution of monogamy in this and other species has resulted from advantages or constraints will require further study.

Bart and Tornes (1989) review a number of male-removal studies and conclude that for species in which the male appears to be helping, survival of the young, and hence female reproductive success, is reduced in his absence. In Eastern Kingbirds, males appear to play an important role in nest defense and in provisioning the young. Our results indicate that this contribution by the male plays a significant role, at least in some years, in determining the reproductive success of the female.

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Nesting ecology of Mourning Doves in a cold desert ecosystem.—Mourning Doves (*Zenaidura macroura*) are distributed widely across the shrub deserts and grasslands of the western United States (McClure 1950), even where there are few or no trees. Doves are adaptable nesters, and a number of studies have dealt with, or mentioned, ground nesting by Mourning Doves (Cowan 1952, Hon 1956, Downing 1959). Fichter (1959) studied Mourning Dove production in four Idaho orchards, and Dahlgren (1955) studied tree-nesting doves in the intermountain region of Utah. However, there have been no published studies relating specifically to ground-nesting Mourning Doves in intermountain shrub deserts. Herein, we provide estimates of Mourning Dove nesting success and identify the vegetative cover variables associated with nest-site selection in ground nesting Mourning Doves in such an ecosystem.

Study area and methods.—Nesting Mourning Doves were studied on the Idaho National Engineering Laboratory (INEL) from 1983 to 1985. The INEL is located 80 km west of Idaho Falls on the upper Snake River Plain in southeastern Idaho and is administered by the U.S. Department of Energy. It encompasses about 231,600 ha at the northern extent of the Great Basin desert and receives 18-20 cm of precipitation annually (Anderson et al. 1978). The major vegetation types of the INEL were reported by McBride et al. (1978). Dominant shrubs on the INEL include big sagebrush (*Artemisia tridentata*) and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*); common grasses include squirrel tail (*Sitanion hystrix*), Indian ricegrass (*Oryzopsis hymenoides*), needle-and-thread grass (*Stipa comata*), and wheatgrasses (*Agropyron* spp.). Common forbs on the INEL include prickly pear cactus