Fitness consequences of helping behavior in the western bluebird

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We examined the fitness consequences of helping behavior in the western bluebird (Sialia mexicana) at Hastings Reservation in Carmel Valley, California, USA, and tested hypotheses for how helpers benefit from engaging in alloparental behavior. Both juvenile and adult western bluebirds occasionally help at the nest. During a 12 year period, all adult helpers and most juvenile helpers were male. Helpers usually fed at nests of both their parents and rarely helped when only one parent was present. The frequency of pairs with adult helpers was only 7%, but nearly one-third of adult males helped among those with both parents on the study area. At least 28% were breeders whose nests failed. The propensity to help appears to depend upon parental survival, male philopatry, and the breeding success of potential helpers. Feeding rates were not increased at nests with juvenile helpers, apparently because breeding males reduced their feeding rates. In contrast, adult helpers increased the overall rates of food delivery to the nest in spite of a reduction in the number of feeding trips made by both male and female parents. Helpers did not derive any obvious direct fitness benefits from helping, but they had greater indirect fitness than nonhelpers due to increases in nesting growth rates and fledging success at their parents' nests. Helpers fledged fewer offspring in their first nests than did nonhelpers, suggesting that they were birds with reduced reproductive potential. Although we have not yet measured the effect of extrapair fertilizations on the fitness benefits of helping, we calculated the difference in fitness between helpers and nonhelpers as a function of the potential helper's paternity when breeding independently and his father's paternity in the nest at which he might help. In conjunction with constraints on breeding and indirect fitness benefits, we predict that relatedness of males to the young in their own as well as their parents' nests will influence helping behavior in western bluebirds.

Key words: Alloparental care, cooperative breeding, helpers, indirect fitness, Sialia mexicana, western bluebird. [Behav Ecol 7: 168-177 (1996)]

Helping behavior has excited the interest of behavioral ecologists because it appears paradoxical that sexually mature animals forego independent breeding to care for the offspring of others. In birds, an estimated 220 species breed cooperatively (Stacey and Koenig, 1990). Most studies of cooperative breeding have focused on species in which helping behavior is common (Brown, 1987; Stacey and Koenig, 1990). However, the proliferation of long-term studies of color-marked populations has revealed a low incidence of helping behavior in some avian species that normally breed as socially monogamous pairs, including European bee-eaters (Merops apiaster, Jones et al., 1991), dusky flycatchers (Empidonax oberholseri, M. Percyra, personal communication), and bush tits (Psaltriparus minimus, Sloane, 1992).

Brown (1980, 1987) clarified analysis of the fitness consequences of helping behavior by suggesting that direct and indirect benefits be assessed separately. Direct benefits are derived from increases in the number of its own offspring an individual produces as a consequence of helping, whereas indirect benefits are increases in inclusive fitness due to production of nondescendent kin (Hamilton, 1964). Emlen and Wrege (1989) used this approach with white-fronted bee-eaters (Merops bullockoides) to test nine different hypotheses for how helpers gain by alloparenting. Their approach provided a rigorous means of analyzing the relative importance of direct and indirect benefits for the evolution of helping behavior and yielded a framework within which to compare helping behavior among species.

Like eastern bluebirds (Sialia sialis), western bluebirds (S. mexicana) are socially monogamous, philopatric, territorial, and sexually dichromatic, with males exhibiting more cobalt blue and orange coloration than females. Although bluebirds have been a symbol of avian monogamy and biparental care, long-term studies of color-marked populations nesting in artificial cavities have revealed departures from classical monogamy in the form of extrapair fertilizations and intraspecific brood parasitism (Gowaty and Bridges, 1991; Gowaty and Karlin, 1984) as well as occasional reports of more than two individuals tending a single nest (Pinkowski 1975, 1976). At Hastings Reservation in upper Carmel Valley, California, USA (36°23′ N, 121°33′ W), western bluebirds exhibit cooperative breeding, with both juveniles and adults helping socially monogamous pairs feed nestlings, defend the nest, and feed fledglings. Here we describe the types of helping behavior exhibited by western bluebirds and present 12 years of demographic data, using the framework provided by Emlen and Wrege (1989), to address the relative importance of direct and indirect benefits of helping at the nest.

MATERIALS AND METHODS

Study population

Western bluebirds are year-round residents at Hastings Reservation. On our study area, socially monogamous pairs defend up to seven nest-boxes from other western bluebirds and violet-green swallows (Tachycineta thalassina). Breeding usually begins in late March, but the first egg of the year has appeared as early as 8 March and as late as 2 May. Most pairs have no more than one successful nest per season, although in 67% of years a small proportion of pairs (less than 20%) attempted second nests after fledging young from their first nests. The female alone incubates and broods the young.
though the male occasionally feeds her on the nest and usually accompanies her on foraging trips. Both males and females feed nestlings and fledglings, with males making nearly half the feeding trips to the nest. Incubation lasts 14 days and most young fledge at 20 days. When both the male and female survive, they almost always stay together from one season to the next. From 1983 through 1994, there were 7 cases of mate-switching out of 117 (6%) cases in which both the male and female bred on the study site for 2 consecutive years and 3 cases of mate-switching out of 106 (3%) renests and second nests within a year.

Nest-boxes were first placed in the field in 1983. The number of nest-boxes was expanded over the next 2 years to a total of 563, at which point the study area encompassed approximately 7 km², including most of Hastings Reservation and part of the adjacent Oak Ridge Ranch. On average, boxes were placed 78.2 ± 51.5 (SE) m from the nearest neighboring box and were placed on trees (n = 325), fences (n = 28), and telephone poles (n = 10).

Monitoring helping and reproductive success

Nest-boxes were cleaned out and broken boxes rebuilt in early March at the start of each field season. Boxes were checked at maximum intervals of 2 weeks for the presence of nest starts. Once found, nests were observed more frequently to identify the birds feeding at the nest, determine the first egg date and hatch date, count eggs, hatchlings, and fledglings, and band nestlings and new adults. Nests found in natural cavities on the study area were also monitored. In all, we monitored 890 western bluebird nests.

Helpers at the nest were identified in three ways. In the early years of the study, we watched nests to determine the identities of birds feeding and detect unbanded adults needing to be caught. Beginning in 1987, 1 h feeding watches were conducted at most nests. After 1989 we conducted two to three 1.5 h feeding watches per nest, distributed among three intervals: 4 to 6 days after hatching, 9 to 11 days after hatching, and 14 to 16 days after hatching. Feeding watches were conducted from a blind or from behind vegetation approximately 30 m from the nest-box. We watched through a spotting scope, recorded the number of feeding trips to the nest, and noted the identities of the birds feeding. When we analyzed feeding rates, we excluded nest watches that were less than 60 min long (mean duration = 86.4 ± 0.3 min, n = 765 watches, for a total of 1105 h of observation). From 1989 through 1991, fledging watches were conducted at 14 nests.

In most cases, identities of putative parents and helpers were determined from color bands; we usually did not know the true genetic relationships between the helpers and the birds they assisted. However, DNA fingerprinting confirmed parentage for four juvenile and six adult helpers that were all genetic offspring of the breeders they assisted, as well as two adult helpers that did not share paternity but assisted their full brothers (Dickinson JL, in preparation). About one-third of nests had at least one extrapair offspring; 16.5% of 115 offspring resulted from extrapair fertilization and less than 1% from intraspecific brood parasitism (Dickinson JL, in preparation).

Fledging success was estimated from the number of nestlings alive at sexing (≥ day 15). An initial, diagnostic color band was put on nestlings on day 6 of the nestling phase. Nestlings received a full complement of color bands on day 13 or 14. Nestlings were weighed when they were handled, usually on days 6 and 14.

Adults born on the study area were classified as yearling, second year (2Y), third year (3Y), fourth year (4Y), and fifth year (5Y) birds. We aged immigrants by the color and shape of the tenth primary (Pitts, 1985) and otherwise designated immigrants as after hatch year (AHY) birds. Immigrants aged as AHY birds were treated as yearlings where specified.

Statistical analysis

Means are presented plus/minus standard error of the mean (SE). Where proportions were used in parametric tests, the data were angularly transformed. Except where otherwise noted, data on feeding rates were analyzed using a two-way ANOVA for the effects of help and nestling age class (1 to 6 days, 7 to 12 days, and more than 12 days after hatching).

RESULTS

Who helps?

Both juveniles and adults helped at the nest. Juvenile helpers were young of the year that helped at their parents' second nests (Figure 1). Second nests occurred in 8 out of 12 years of the study. All but three juvenile helpers (86.4%) and all adult helpers (100%) were male.

The sex difference in helping frequency was analyzed as the proportion of individuals that helped of those that had the opportunity to help. In the case of juveniles, we assumed that all fledglings whose parents had a second nest that year had the opportunity to help. Male juveniles were more likely than female juveniles to help at their parents' second nests; the frequency of 3 helpers among 91 (3.2%) female fledglings was statistically lower than the frequency of 19 helpers among 106 (17.9%) male fledglings (χ² = 9.1, p = .003).

We assumed that the opportunity for adult western bluebirds to help their parents depends on two factors: (1) whether the potential helper was present on the study area as an adult and (2) whether both of his or her putative parents were present on the study area. Male nestlings are four times as likely as female nestlings to return to the study area to breed (Koenig WD and Dickinson JL, unpublished data). No adult...
females helped. The frequency of 0 female helpers out of 19 returning females with both parents alive was statistically lower than the frequency of 24 male helpers out of 80 adult males with both parents alive, indicating that females are less likely to help even when they are philopatric and both parents are present ($\chi^2 = 6.0, p < .02$).

Among males with the opportunity to help both parents, the frequency of adult males helping was higher than the frequency of juvenile males helping, but the difference was not statistically significant when we considered all adult males ($\chi^2 = 2.5, N = 186, p = .11$), nor was it significant when we restricted analysis to 2Y males ($\chi^2 = 4.2, N = 176, p = .27$).

In 12 years, only 19 banded juveniles helped out of 106 (17.9%) male fledglings whose parents had second nests, whereas adult males helped in 24 out of 80 (30%) cases where they had both parents on the study area. Although there were only 10 cases of 3Y and 4Y males with both parents on the study area, males helped in 5 (50%) of these cases. The frequency of adult males helping when both parents were alive did not differ between the 2Y and >2Y age classes, indicating that age of the male does not influence whether or not he helps (Fisher's Exact test, $p = .10$).

In 47% of 32 cases where the helper was previously banded, adult helpers either bred or attempted to breed during the same season they helped. In six of these cases (19%), helpers also fed at their own, simultaneous nests on nearby territories, while in nine cases (28%) the males helped only after their own nests failed. One male fed as a replacement male at a widowed female's nest while also helping his parents.

How do helpers help?

We observed three types of helping behavior: feeding of nestlings, feeding of fledglings, and nest defense. Feeding of nestlings accounted for all but one occurrence of helping behavior described in Figure 1. In addition, three adult helpers and three juvenile helpers fed fledglings at four nests that were watched during the fledgling stage in 1989 through 1991. All but one of these helpers fed nestlings as well; the helper that did not, fed fledglings after he abandoned his own nest. This was an unusual case where he may have had paternity since he was present on his natal territory and consorted with his father and stepmother prior to and during egg laying. He also may not have had paternity in the nest he abandoned, since it was a late nest with a widowed female that had previously copulated with her earlier mate and received copulation attempts from two other males. In addition to feeding nestlings and fledglings, helpers participated in nest defense by calling, swooping, and hovering.

Feeding rates at nests with and without helpers

$\textbf{Adult helpers}$

When present, adult helpers contributed approximately one-third of the feeding trips and increased the feeding rates at their parents' nests (Figure 3a). Nestlings received more feeds at nests with helpers, even though male and female breeders fed at lower rates when helpers were present than when they were not (Figures 3a, b). Because helpers and male breeders were difficult to distinguish during some watches, we used only the 740 watches where the feeder's identity was known for each visit to the nest. Hourly feeding rates for breeders were lower at helped than unhelped nests, but the result was only marginally significant for males (two-way ANOVA: male—$F_{1,754} = 3.7, p = .05$; female—$F_{1,754} = 5.9, p = .01$; Figure 3a). The number of nestlings present was higher for nests with helpers than nests without helpers (two-way ANOVA (help and nestling age): helper effect—$F_{1,754} = 4.1, p = .04$; Figure 4). In a three-way ANOVA of the effects of helper, nestling age class, and the number of nestlings, both males and females made fewer feeding trips per hour when helpers were present than when they were not (helper effect: male—$F_{1,750} = 6.5, p = .01$; female—$F_{1,750} = 7.6, p = .006$; Figure 3a). The hourly feeding rates of male and female parents were also significantly lower on a per nestling basis when helpers were present than when they were not (two-way ANOVA (help and nestling age), feeds per nestling per hour: males—$F_{1,750} = 7.5, p = .006$; females—$F_{1,750} = 8.9, p = .003$; Figure 3b).

Both the total feeds per hour and the total feeds per nestling per hour were statistically higher at 42 first nests with adult helpers than at 725 first nests without helpers (two-way ANOVA: total feeds/h—$F_{1,750} = 9.2, p = .002$; total feeds/nestling/h—$F_{1,750} = 4.5, p = .03$; Figure 3a,b). Overall feeding rates also increased significantly with nestling age (total feeds per hour: $F_{3,358} = 38.2, p < .001$; total feeds per nestling per hour: $F_{3,358} = 37.7, p < .001$).

$\textbf{Juvenile helpers}$

In contrast with adult helpers, juvenile helpers contributed only 21% of the feeding trips and had little effect on food
Figure 3
(a) Hourly feeding rates (feeds/h) for first nests with and without adult helpers. (b) Nestling feeding rates (feeds/nestling/h) for first nests with and without adult helpers. (c) Hourly feeding rates (feeds/h) for second nests with and without juvenile helpers. (d) Nestling feeding rates (feeds/nestling/h) for second nests with and without juvenile helpers.

The relationship between density of pairs and helping behavior

We examined the relationship between the density of pairs and two different measures of the frequency of helping by adults in the years from 1984 to 1994. The frequency of pairs with helpers ranged from 0% to 16% (mean = 7.4 ± 1.2%, N = 11 years). Western bluebirds occupied fewer than 36% of available nest-boxes from 1983 through 1994 (Figure 5a). The mean (± SE) number of pairs on the study area was 56.2 ± 8.9 (range 33 to 125) after 1984, when all of the nest-boxes were in place. The frequency of adult helpers, measured as the proportion of pairs having at least three adults feeding at the nest, was not statistically correlated with the density of pairs (Spearman rank correlation: r_s = -.36, n = 11, p = .25). Using an alternative measure of adult helper frequency—the proportion of adult males that helped their parents of all males with both parents on the study area—helper frequency was still not significantly correlated with the density of pairs (Figure 5b). Correlation coefficients for both these measures were negative and opposite the direction expected if helping behavior is caused by elevation of nest densities due to use of nest-boxes.

Why do adult males help?

Because adult helpers potentially sacrifice breeding opportunities, we restricted our analysis to the fitness benefits of helping behavior by yearling and older western bluebirds. Table 1 shows hypothesized direct and indirect fitness benefits of helping at the nest.
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Figure 4
Number of nestlings counted after feeding watches at 741 first nests with (n = 38) and without (n = 703) adult helpers and 79 second nests with (n = 20) and without (n = 59) juvenile helpers.

Direct fitness benefits for adult helpers
Enhanced survival of birds that help. Helpers might derive survival benefits due to increased group size (Brown, 1987) or because they are safer on the familiar, natal territory (Gaston, 1978). These hypotheses predict that survivorship of helpers is greater than that of nonhelpers. However, adults that helped had lower return rates than adults that bred and return rates for the two groups were not statistically different (Table 2).

Enhanced future probability of breeding. Future probability of breeding could be enhanced if helpers later disperse in coalitions with siblings they helped rear (Ligon and Ligon, 1978), inherit mates (Reyer, 1980), or if helping enhances their ability to obtain a breeding territory (Woolfenden and Fitzpatrick, 1984). Our data do not support the first two hypotheses, because no adult helpers formed coalitions with nestlings they helped raise and no helpers later bred with the female they assisted.

Helping could facilitate obtaining a breeding territory or nest cavity in three ways: 1) males might inherit their parents’ territory or a piece of it through territorial budding (Woolfenden and Fitzpatrick, 1984); 2) coalitions of relatives might cooperate in aggressive behaviors that push back the boundaries of a neighbor’s territory and open up a vacancy; or 3) helpers might be better able to compete for a vacancy because their parents’ territory affords them access to superior food, roosting sites, or cooperative vigilance and antipredator defense. These hypotheses predict that helpers will breed closer to where they helped than nonhelpers breed relative to their natal site. Helpers did not nest a shorter distance from where they helped than nonhelpers nested relative to their last contact with their parents (Mann-Whitney U = 1994, n₁ = 17 helpers, n₂ = 175 nonhelpers, p = .67), nor was natal dispersal distance shorter for helpers than nonhelpers (Mann-Whitney U = 1412, n₁ = 17 helpers, n₂ = 175 nonhelpers, p = .73). Males that helped as adults were older when they initiated breeding than males that did not help, including nonhelpers that disappeared for a year or two, then bred (Table 3).

Increased breeding success. Helpers may gain if the nestlings they raise later assist them at their own nests (Ligon and Ligon, 1978) or if the experience they acquire increases their reproductive success (Emlen and Wrege, 1989). The first hypothesis is unlikely to explain helping behavior in western bluebirds as no nestling reciprocated by later helping at the nest of an adult auxiliary feeder (Figure 2).

To examine the second hypothesis, we compared the reproductive success of helpers with that of nonhelpers using only birds that were born on the study area and survived to breed. Contrary to the prediction of the experience hypothesis, the proportion of successful nests for males that helped was statistically lower than the proportion of successful nests for males that did not help (Table 3). Furthermore, helpers fledged fewer young in their first nests than did nonhelpers (Table 3). A two-way ANOVA that included the effect of age at first breeding also indicated that when they bred on their own, helpers had lower nesting success than nonhelpers (proportion of successful nests: F₁,150 = 5.53, n = 157, p = .02; young fledged in first breeding attempt: F₁,150 = 3.70, n = 157, p = .056).

Adult helpers did not have lower lifetime reproductive success than nonhelpers. Helpers had more nesting attempts and bred longer than nonhelpers and, although these differences were not statistically significant, they appeared to compensate for the delayed onset of breeding and reduced nesting success.

Figure 5
(a) The number of western bluebird pairs and boxes for 12 different years of the study. (b) The relationship between the frequency of males helping of those with both parents present on the study area and the density of nesting pairs (Spearman rank correlation, r = −.07, p = .79).
Prediction not tested here for lack of data on extrapair fertilizations. Hypothesis supported.

Hypothesis not supported.

AHY
Age

Table 2
Survivorship to the next year of helpers versus breeders

<table>
<thead>
<tr>
<th>Age</th>
<th>Breeders</th>
<th>Helpers</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>AHY</td>
<td>48.3% (118)</td>
<td>33.5% (5)</td>
<td>0.94, ns</td>
</tr>
<tr>
<td>2Y</td>
<td>41.1% (128)</td>
<td>40.0% (15)</td>
<td>0.86, ns</td>
</tr>
<tr>
<td>3Y+</td>
<td>49.8% (201)</td>
<td>20.0% (5)</td>
<td>0.39, ns</td>
</tr>
</tbody>
</table>

Numbers in parentheses are sample sizes; ns $p > .25$.

Table 3
Comparison of direct fitness components for adult helpers ($N = 19$) versus nonhelpers ($N = 140$) that were born on the study area and survived to breed

<table>
<thead>
<tr>
<th>Fitness component</th>
<th>Helpers</th>
<th>Nonhelpers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of nests successful</td>
<td>$0.44 \pm 0.10$</td>
<td>$0.67 \pm 0.05$</td>
</tr>
<tr>
<td>Young fledged in first nest</td>
<td>$2.00 \pm 0.61$</td>
<td>$3.19 \pm 0.22$</td>
</tr>
<tr>
<td>Age first bred, years</td>
<td>$1.65 \pm 0.23$</td>
<td>$1.13 \pm 0.03$</td>
</tr>
<tr>
<td>Years bred</td>
<td>$1.84 \pm 0.27$</td>
<td>$1.79 \pm 0.08$</td>
</tr>
<tr>
<td>Nesting attempts</td>
<td>$2.74 \pm 0.52$</td>
<td>$2.26 \pm 0.11$</td>
</tr>
<tr>
<td>Successful nests</td>
<td>$1.47 \pm 0.41$</td>
<td>$1.50 \pm 0.09$</td>
</tr>
<tr>
<td>Young fledged</td>
<td>$5.58 \pm 1.69$</td>
<td>$6.20 \pm 0.40$</td>
</tr>
</tbody>
</table>

$p < .05$.

$** p < .001$.

ns, $p > .05$, Mann-Whitney $U$ test.

(Table 3). Although they fledged 0.62 fewer offspring on average than nonhelpers, helpers did not exhibit a statistical reduction in the total number of successful nests they had or the total number of young they fledged during their lifetimes (Table 3). This result was also supported by a two-way ANOVA that included the effect of birth year.

Indirect fitness benefits for adult helpers

Relation of between breeders and helpers. Assuming genetic monogamy, helpers usually fed siblings and, more rarely, nieces and nephews (Figure 2). They were more likely to help when both their social parents were breeding together than when one or no parent was present (Table 4). When the data were restricted to males with at least one parent alive, this result was still statistically significant ($\chi^2 = 30.8, n = 207, df = 2, p < .001$). This pattern is consistent with a preference of helpers to help raise close kin than distantly related kin. 

Increased survival of breeders. Helping may increase breeder survival if it reduces the amount of work breeders do or the risks associated with parental care (Emlen and Wrege, 1989). When an adult helper was present, the feeding rates of both male and female breeders were reduced (Figure 3, analysis above).

We compared return rates of breeders that had at least one helper with return rates of breeders that had no helpers, excluding 2Y and AHY breeders, which have no adult offspring that could potentially help. The age distributions did not differ between the two groups (Kolmogorov-Smirnov test, females: $z = 0.15, n = 197, p > .5$; males: $z = 0.97, n = 205, p > .8$). Among birds in their third year or older, 54.8% of 31 females returned in year $n + 1$ after receiving help in year $n$, whereas 47.0% of 166 females returned after breeding without a helper. The percentage returning of 32 males that received help was 46.9%, whereas 52.6% of 173 males returned one year after they bred without help. The difference in return rates was not statistically significant for either sex (females: $x^2 = 0.37, n = 197, p > .5$; males: $x^2 = 0.16, n = 205, p > .65$).

Increased reproductive success of breeders. We analyzed the effect of helpers on nestling mass and fledging success to determine whether there might be indirect fitness benefits through enhanced survival of young in nests with helpers. Mean nestling mass was higher at nests with helpers than at nests without helpers matched by nesting age, year, laying
Three helped at their brothers' nests.

A significant proportion of adult helpers helped only after between helper frequency and die weight of 6 day old nest-from years 1984 dirough 1994, we examined the relationship higher in bad years. Using a Spearman rank test and data of a bad situadon in years when diere are constraints on

correlated widi helper frequency. If helping is making the best from nests widi helpers was not statistically different from die widi helpers were not more likely than unaided pairs to at-

tion of fledglings returning to the study area the next year

We did not consider the effect of clutch size, because the presence of a helper did not affect mean clutch size in an ANCOVA of the effects of year and help, controlling for first egg date (ANCOVA: help: $F_{1,607} = 0.7$, $n = 631$, $p = .4$; year: $F_{1,607} = 3.3$, $n = 631$, $p < .001$; first egg date: $F_{1,607} = 64.6$, $n = 631$, $p < .001$).

On average, first nests with helpers fledged 1.12 more off-spring than first nests without helpers (nests with helpers: 3.87 ± 0.30 fledglings; nests without helpers: 2.75 ± 0.09 fledglings). However, this value includes the association between help and nest success or failure, as well as the association between help and the number of young fledged from successful nests. The presence of a helper was associated with success in fledging at least one offspring ($x^2 = 7.14$, $n = 615$, $p < .01$). However, when nests that failed were excluded from the sample, nests with helpers still had significantly higher fledging success than nests without helpers (Table 5). Parents with helpers were more likely than unaided pairs to attempt a second nest after a successful first nest. Only 2 of 42 pairs (5%) with helpers attempted a second nest in years with second nests, whereas 26 of 305 successful pairs (9%) without helpers attempted to nest again (Fisher’s Exact test, $p = .19$).

**Increased survival of fledglings to breeding age.** The proportion of fledglings returning to the study area the next year from nests with helpers was not statistically different from the proportion of fledglings returning from nests without helpers (males: $x^2 = 2.14$, $n = 946$, df = 1, $p = .15$; females: $x^2 = 0.9$, $n = 845$, df = 1, $p = .34$). Only 15% of male fledglings returned from nests with helpers as compared with 23% from nests without helpers. In contrast, 8% of female fledglings returned from helped nests as compared with 5% from un-helped nests.

**Constraints on breeding**

A significant proportion of adult helpers helped only after their own nests failed. We examined four potential indicators of constraints on breeding to determine whether they were correlated with helper frequency. If helping is making the best of a bad situation in years when there are constraints on breeding, the proportion of adult males helping should be higher in bad years. Using a Spearman rank test and data from years 1984 through 1994, we examined the relationship between helper frequency and the weight of 6 day old nestlings, the proportion of first nests and all nests that were suc-

cessful, and the number of young fledged per successful nest. These four indicators of breeding hardship were negatively correlated with the frequency of adult males helping (of those that still had both parents alive), with $r < -.7$ and $p = .02$ for proportion of first nests successful and young fledged per successful nest. However, the results were not statistically significant using a sequential Bonferroni technique [all $p > .05/ (1 + k = i)$, where $k = 4$ (the number of tests) and $i = rank$ of $p$ from .02 to .83]. Although not significant with multiple comparisons statistics, the direction of these results is consis-

tent with the hypothesis that helper frequency is higher in years when breeding is difficult.

**DISCUSSION**

**Helping behavior in western bluebirds**

Isolated reports of helping behavior in eastern bluebirds in-

dicate that deviations from singular breeding are rare (Pin-

kowski, 1976, 1977). In western bluebirds, helping occurs in some populations, but not others. Stierhoff (1984) studied western bluebirds in nest-boxes in Coconino County, Arizona, USA, from 1982 to 1984. He observed helping behavior at a frequency similar to that found in this study. In contrast, Mock (1990) did not observe helping behavior in a 4 year study of color-banded western bluebirds in Riverside County, Califor-

nia, USA.

Juvenile helpers were not more common than adult help-

ers, even though juveniles do not have the option of breeding. On our study area, the mean percentage of pairs with adult helpers was 7.4 ± 1.2% (range 0% to 16% across years). How-

ever, 30% of adult males helped when both their parents were present on the study area. The high incidence of helping among adult males with both parents alive begs the question of whether helping is uncommon in eastern bluebirds and in some populations of western bluebirds simply because opportunities to help both parents are rare. Alternatively, there may be differences in rates of nest failure or other factors influencing the costs and benefits of helping behavior (Koenig et al., 1992).

<table>
<thead>
<tr>
<th>Table 4</th>
<th>The frequency of adult males helping with both parents, one parent, and no parents present on the study area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Helped</td>
<td>Did not help</td>
</tr>
<tr>
<td>Both parents breeding</td>
<td>24*</td>
</tr>
<tr>
<td>Only father breeding</td>
<td>3b</td>
</tr>
<tr>
<td>Only mother breeding</td>
<td>1</td>
</tr>
<tr>
<td>No parents breeding</td>
<td>4c</td>
</tr>
</tbody>
</table>

$x^2 = 48, N = 321, df = 5, p < .001.$

* One helped at his brother's nest.

b One helped at his brother's nest (excludes son that defended but did not feed).

c Three helped at their brothers' nests.

date, and number of hatchlings (Wilcoxon matched-pairs signed-rank test: $z = -2.47, n = 29$ pairs, $p = .01$).

Fledging success is a product of the proportion of successful nests and the number of fledglings per successful nest. We excluded from analysis nests that were not watched carefully enough to determine whether a helper was present or not. We did not consider the effect of clutch size, because the presence of a helper did not affect mean clutch size in an ANCOVA of the effects of year and help, controlling for first egg date (ANCOVA: help: $F_{1,607} = 0.7$, $n = 631$, $p = .4$; year: $F_{1,607} = 3.3$, $n = 631$, $p < .001$; first egg date: $F_{1,607} = 64.6$, $n = 631$, $p < .001$).

The propor-

**Table 5**

Results of two-way ANCOVA of number of fledglings per successful nest using year and presence or absence of an adult helper as main factors and first egg date as a covariate

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Year</th>
<th>Helper</th>
<th>Interaction</th>
<th>First egg date</th>
<th>Explained</th>
<th>Residual</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sums of squares</td>
<td>624.6</td>
<td>290</td>
<td>81.8</td>
<td>100.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>df</td>
<td>309</td>
<td>3.5</td>
<td>14.0</td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F$ value</td>
<td>18.0</td>
<td>19</td>
<td>18.2</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent of total variance</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Main factors</td>
<td>Year</td>
<td>84.7</td>
<td>11</td>
<td>6.0</td>
<td>**</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Helper</td>
<td>5.9</td>
<td>1</td>
<td>4.1</td>
<td>**</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Interaction</td>
<td>Year by helper</td>
<td>8.7</td>
<td>10</td>
<td>0.7</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Covariate</td>
<td>First egg date</td>
<td>18.0</td>
<td>1</td>
<td>14.0</td>
<td>**</td>
<td>—</td>
<td></td>
</tr>
</tbody>
</table>

* $p < .05$.

** $p < .001$, all other $p > .05$; multiple $r^2 = 0.17$. [174] Behavioral Ecology Vol. 7 No. 2
Direct and indirect fitness benefits of helping

We found no evidence supporting the hypothesis that helpers gain direct fitness benefits from helping (Table 1). Helpers did not gain survival and breeding advantages in later years as a consequence of helping. In fact, lifetime reproductive success of adult helpers was 0.62 offspring lower than that of males that never helped, although the difference between the two groups was not statistically significant (Table 3). Although helping did not appear to enhance future breeding opportunities, it is possible that males incur cryptic fitness benefits by helping. For example, young males may gain extrapair fertilizations from helping by using the natal territory as base from which to seek extrapair copulations with neighboring females. DNA fingerprinting revealed that over one-third of nests have at least one extrapair offspring (Dickinson JL, in preparation). However, the fitness effects of covert breeding can only be evaluated using single-locus markers to assign paternity of large numbers of extrapair offspring, something we have not yet done.

Our evidence supports the hypothesis that helping behavior in western bluebirds has been shaped, in part, by indirect fitness benefits (Table 1). Adult males are less likely to help when one parent has died. A tendency for helpers to raise full sibs over half sibs is an important prediction of the hypothesis that helps gain indirect fitness benefits. Our data do not permit us to discriminate between the hypothesis that helpers prefer to help both parents and the hypothesis that sons from prior nests are evicted when parents are widowed. However, the ultimate consequence of the pattern we observed is that helpers are more likely to assist in raising close than distant relatives.

Helpers did not derive future indirect fitness benefits (Mumme et al., 1989) through increases in parental survival, even though breeders fed less when there was an adult helper at the nest. However, nests with helpers had higher nestling growth rates, greater probability of success, and fledged more young than nests without helpers. We were unable to detect any difference in recruitment into the population from nests with helpers versus nests without helpers, but this is not surprising given the low return rates of fledglings and the possibility that birds in better condition disperse farther. Because we cannot distinguish death from dispersal, we cannot devise a convincing test for the effect of helping on overwintering survival of fledglings.

If birds that help are those with inferior reproductive potential, it is possible that individual helpers derive greater inclusive fitness benefits than are indicated by the observational data. To examine this possibility, we would have to create a new class of helpers by inducing nest failure in birds attempting to breed and create a new class of nonhelpers by removing the parents of birds attempting to help. Only then could we compare the performance of breeders with the performance of a similar class of birds prevented from helping.

Helping—a plastic response with variable payoffs?

Two lines of evidence suggest that constraints on breeding favor helping behavior in western bluebirds. First, 15 of 32 (47%) banded adult helpers were seen attempting to breed in the year when they helped and 9 (28%) helped only after their own nests failed. As was suggested for white-fronted bee-eaters (Emlen and Wrege, 1989) and European bee-eaters (Lessels, 1990), helping in western bluebirds appears to be a means by which birds increase their fitness in the event of breeding failure. Second, male removal experiments indicate that there are color-banded floater males (sensu Brown 1987, p. 299) that act as “replacement males” (Meech and Robertson, 1991, 1992). The occurrence of replacement males suggests that breeding opportunities are limiting for males. Replacement males sometimes retain the territory and mate with the female during her subsequent nesting attempt, suggesting that acting as a replacement male may be a route to finding a mate (Dickinson JL, unpublished data).

Helping may be a default strategy for western bluebird males that are unable to attain breeding status due to nest failure, loss of mate, or inability to find a mate in the first place. This interpretation is similar to that of Rager (1990) for pied kingfishers (Ceryle rudis). Rager suggested that males that are unable to find reproductive vacancies become primary helpers if their parents are alive and become less hard-working secondary helpers at the nests of unrelated pairs if their parents are not living. In western bluebirds, males don’t become secondary helpers, but instead remain on the study area as nonbreeders or, when the opportunity arises, act as replacement males at nests of widowed females.

Using data from 11 years, we found no general indicator of constraints on breeding that was statistically correlated with the frequency of helpers. This may be because the decisions of males to help are influenced by a diversity of factors, which should be considered in explaining the constraints on breeding that we have not yet evaluated is the threat of extrapair fertilizations. Approximately 16.5% of 115 offspring examined with multilocus DNA fingerprinting were sired by males other than the caregiving males (Dickinson JL, in preparation). In one nest, all three nestlings resulted from extrapair fertilization. Helpers did not have paternity in the nests at which they helped, even when the recipient of help was their brother. Extrapair fertilizations are frequent enough to figure importantly in measures of reproductive success for male western bluebirds at Hastings Reservation. If young males have more extrapair offspring in their nests than older males, they might achieve higher inclusive fitness by helping to increase the fledging success at their parents’ nests. Even young males’ half sibs in the nest of the male’s nest may prove superior to rearing unrelated offspring in a male’s own nest.

Helping may be conditional, such that males are more likely to help when the frequency of extrapair fertilizations in their own nest is high. Low paternity in the nests of young males may even explain why six males helped while they had active nests of their own. Behavioral plasticity in feeding allocation could come about through rules similar to those used by dunnocks (Prunella modularis), in which male allocates parental care in accordance with the amount of reproductive access they have to the female during her fertile period and their consequent paternity (Davies et al., 1992).

The potential effects of extrapair paternity on the fitness consequences of helping versus not helping are shown in Figure 6, which is based on single-season estimates of fitness for individuals that attempt to breed but do not help versus individuals that both attempt to breed and help their parents. Fledging success at nests of helpers and nonhelpers was calculated from the success of first breeding attempts for these two groups of birds. We calculated success of helped and unheloped breeders using males that were at least 3Y birds, and thus could potentially have adult helpers. Because intraspecific nest parasitism is rare in the Hastings population (less than 1%), we assumed that maternity was always 100% (Dickinson JL, in preparation). Fitness of helpers relative to nonhelpers varies with both paternity of helpers in their own nests and paternity of their parents in the parental nest (Figure 6). If a male’s paternity is 0 to 0.5, the helper benefits by assisting his parents. If paternity in his own nest is 0 or 0.25, then he does better by helping his parents, even if an
unrelated male sires all of the offspring in his father's nest. This is because he will be helping to raise young to which he is related by 0.25 through his mother.

As Figure 6 illustrates, a male with proportional paternity in his own nest equal to 1.0 always does better by not helping. This provides one explanation for why adult females do not help. Because intraspecific brood parasitism is rare, females have high confidence of maternity and, all else being equal, will always do better by channeling resources into their own offspring. A second reason why females do not help may be that breeding opportunities are not as constrained as for males. We have never seen a replacement female, but have yet to conduct female removal experiments to determine whether there are more males available to fill vacancies than females.

We hypothesize that three primary constraints on breeding favor helping by adult males: breeding failure, a shortage of females, and the inability of some males to protect their paternity. Although the overall frequency of helping in western bluebirds is low, nearly one-third of males help of those that have both parents alive. The reproductive costs of helping are reduced because some birds help and breed at the same time. Fitness calculations indicate that the indirect benefits of helping yield the greatest fitness gains when helpers sire few young in their own nests and when their father’s paternity is high in the nest receiving their help (Figure 6). However, males may gain direct paternity benefits that are not accounted for in this model if they acquire extrapair fertilizations as a consequence of remaining on their parents' territory. By determining parentage of large numbers of families exercising different reproductive options, we will be able to test the hypothesis that males base their allocation of parental care, as breeders, helpers, and replacement reproductives, on a complex of information about their breeding success, relatedness, and opportunities for parentage.

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