

## Influence of nest-site and individual quality on breeding performance in Merlins *Falco columbarius*

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We examined the effects of nest-site quality and bird quality on breeding performance in male and female Merlins *Falco columbarius* from a long-term study in Saskatoon, Saskatchewan. In addition, we tested whether nest-site quality was associated with survival, as well as lifetime reproductive success (LRS). For females, nest-site quality had little influence on any of the measures of breeding performance or survival. Even so, when females switched nest-sites, they tended to move to better ones. Hatch date was repeatable for the same females occupying different nest-sites but not for the same sites occupied by different females. Among males, birds surviving past each age category tended to occupy nest-sites of higher quality, and LRS was positively correlated with nest-site quality. The relationship between nest-site quality and LRS was heavily influenced by the poorest nest-sites. When males switched nest-sites, they too tended to move to ones of higher quality. In addition, chick hatch date was repeatable neither for the same males occupying different sites nor for the same sites occupied by different males. As with most other raptors, male Merlins provide most of the food for the pair and their young during the breeding season, and differences in nest-site quality may have affected the effort needed by males to secure food. Female Merlins, however, appear still to have considerable control over the timing of breeding.

Differential breeding performance in birds is attributable to some degree to differences in either the quality of the birds themselves or the quality of the habitat used for breeding. Most studies concentrate on one of the two aforementioned areas without considering the other (but see Högstedt 1980, van Noordwijk *et al.* 1980, Newton & Marquiss 1984, Goodburn 1991).

The breeding habitat of most species is not uniformly distributed in space and time, but rather, occurs as discrete patches. As habitat changes, it becomes either more or less suitable for certain species to breed in. This territory quality is thought to be a major factor in determining breeding performance in many territorial animal species (reviews in Newton 1992, 1998, Rodenhouse *et al.* 1997). For example,

the majority of land birds (81% of non-passerines and 84% of passerines) breed in pairs on territories (Lack 1968). Territories may differ widely in what they provide to their occupants (e.g. food resources, a refuge from predation, a nest-building site, etc.; Rodenhouse *et al.* 1997). Among raptors, various studies have linked breeding performance and survival to nest-site or territory quality (Korpimäki 1989, Newton 1991, Valkama & Korpimäki 1999, Jenkins 2000, Aparicio & Bonal 2002, Hakkarainen *et al.* 2002, Laaksonen *et al.* 2002). Most authors have suggested that food availability is a key component of quality.

Various lines of evidence have been used to infer the existence of variation in territory and nest-site quality in bird studies. These have been summarized by Ens *et al.* (1992). When one is not able to link habitat quality directly to habitat features or critical resources, one of the most common procedures is to

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rank territories or nest-sites on the basis of the frequency of occupancy during the study period. In previous studies, typically, a positive relationship has been found between the territory rank or quality and breeding performance (Newton 1991, 1998, Ens *et al.* 1992).

Life-history theory predicts that parents should balance their current investment in offspring against their chances of survival and future reproduction (reviewed in Roff 1992, Stearns 1992), and thus an individual's abilities are related to its evolutionary fitness. In some birds, breeding performance depends more on direct input from foraging than on body reserves (Drent & Daan 1980, Winkler & Allen 1996) and, in more abstract terms, the capability or 'quality' of specific birds (e.g. in terms of foraging skills, nest defence ability, etc.; Coulson 1968, Coulson & Porter 1985, Coulson & Thomas 1985, Slagsvold & Lifjeld 1990, Goodburn 1991, Riddington & Gosler 1995, Potti *et al.* 1999, Nordahl & Korpimäki 2002).

Our principal objective in this paper was to test for the effects of nest-site quality and individual quality on breeding performance in Merlins *Falco columbarius*. From a review of the literature, we predicted that birds on better nest-sites would have earlier chick hatch dates and larger broods. We also tested whether nest-site quality was associated with survival and a more general measure of fitness such as lifetime reproductive success (LRS). For nest-site quality we predicted that there existed a positive relationship with survival and LRS.

In addition to the above tests, we used repeatability analysis to determine the relative influence of specific individuals or specific nest-sites on hatch date and brood size.

## MATERIALS AND METHODS

### Study species and area

The Merlin is a small, bird-eating falcon that breeds throughout the northern forests and prairies of North America and Eurasia (Sodhi *et al.* 1993). As part of a long-term population study, from 1985 to 1995, breeding Merlins were live-trapped during the nestling period (June to early July) in Saskatoon, Saskatchewan, Canada (52°07'N, 106°38'W). For a detailed description of the trapping methods and the study area, see Warkentin and James (1988) and James *et al.* (1989). Morphological and reproductive data were collected throughout the period. Any birds captured in 1996 or 1997 were excluded from

all data analyses because they may still have been alive at the end of the study period (Newton & Rothery 1997, Espie *et al.* 2000) and thus would have biased our estimates of breeding performance (in particular LRS).

There is an abundance of House Sparrows *Passer domesticus* in Saskatoon, the primary prey species of Merlins in the region (Sodhi & Oliphant 1993). Like other raptors, Merlins are unusual among birds in that males appear to invest substantially more energy in offspring than do females (Wijnandts 1984, Masman *et al.* 1988). During the incubation period, female Merlins are largely inactive, leaving the nest for only brief periods to feed. By contrast, males are very active, providing most of the food for the female as well as for themselves. Males also provide most (Temple 1972), if not all, of the food during the nestling period (Sodhi *et al.* 1992). Perhaps as a consequence of this, most male Merlins delay breeding until they are 2 years of age whereas most females show no delay and begin breeding at age 1 (Lieske *et al.* 1997, Espie *et al.* 2000).

Reproductive data were derived from 378 captures of 129 individual females and 101 individual males. Breeding males could be aged precisely if they had been banded as nestlings or if they were caught in their first year, when they are separable from adult males (age 2+) on plumage features (Temple 1972). Adult males unbanded at the time of first capture were assigned a minimum age of 2 years (Espie *et al.* 2000). The age of females could be determined precisely only if they had been banded as nestlings.

### Quantification of nest-site quality

As in other falcons, the Merlin does not build its own nest. A previous study of nest-site selection revealed that Merlins in Saskatoon show a preference for breeding in old nests of the American Crow *Corvus brachyrhynchos* in the numerous spruce trees *Picea* spp. that have been planted in residential areas (Warkentin & James 1988).

Following Newton (1991), we based an assessment of nest-site quality on the temporal occupancy of nest-sites. Because Merlins do not build their own nests, we determined nest-site occupancy by noting whether a given nest was closer to a known nest used in any previous year or to its nearest neighbour in the same year. If a nest was closer to an old nest-site then the pair was classified as occupying that 'old' nest-site. If a nesting pair was closer to its nearest neighbour during that year then we classified it as a

'new' nest-site (Espie *et al.* 1996). To account for changes in nest-site quality over time, we graded each nest-site by giving it a separate score for each year, depending on its occupancy in a moving 5-year period, centred on the year in question (Newton 1991, Espie *et al.* 1996). For example, nest-sites in 1987 were given a score (1–5) equal to the number of years occupied in the period 1985–89. Nest-sites for the last 2 years of study were graded on occupancy in the last 5 years of the study. To examine the effect of nest-site quality on LRS we used the average score of all known nest-sites occupied by a bird during its lifetime.

### Measurement of breeding performance

We measured three parameters to assess breeding performance in Merlins. (1) Brood size: the number of chicks (at the time of banding) produced by an individual male or female in each year it was captured. (2) Hatch date: calculated by backdating from the age of the chicks at the time of banding. Ages were determined by comparison with an ageing scheme developed for Merlins by us from captive rearing studies and observations of wild birds. (3) LRS: the total number of young produced over an individual's lifetime (Newton 1989).

A true measure of LRS requires data from complete life cycles; however, owing to the nature of natal dispersal in many species (including most birds) these data are difficult to obtain (Barrowclough & Rockwell 1993). It has been reasoned therefore that lifetime production of fledglings may provide a reasonable approximation in most circumstances (Newton 1989). However, the number of young resulting from extra-pair fertilizations could bias estimates of LRS (Weatherhead & Boag 1997). In our population of Merlins, extra-pair copulations have been observed (Sodhi 1991), but DNA fingerprinting from 20 broods revealed no cases of extra-pair fertilizations (Warkentin *et al.* 1994).

Breeding dispersal (i.e. distance moved between successive breeding attempts) for females in Saskatoon was on average 2.3 (sd =  $\pm$  1.83) km and males moved a mean of 1.1 (sd =  $\pm$  0.90) km (James *et al.* 1989). Thus, a few individuals breeding near the end of the study period may have evaded capture; however, this group was probably very small given our level of capture success (Lieske *et al.* 1997) and given that we allowed two additional years for recapture. On average, we recaptured 57.2% of nesting males and 84.5% of nesting females in each year (Lieske

*et al.* 1997). Therefore, the values of LRS reported should be considered as estimates.

### Analyses

In all instances we analysed the data for males and females separately. As brood size and lifetime reproductive success were not normally distributed ( $P < 0.01$ , Kolmogorov–Smirnov tests and also visual inspection of the data), neither as original data nor when transformed ( $\log_{10}[x + 1]$ ), we used non-parametric tests and randomization methods for most analyses involving these measures (Zar 1984, Siegel & Castellan 1988, Crowley 1992, Adams & Anthony 1996, Manly 1997a). We also excluded zero values from our analyses involving brood size ( $n = 6$ ) and lifetime reproductive success ( $n = 2$ ). We did this because complete breeding failures (once eggs had been laid) in our study were known to be due exclusively to stochastic events (i.e. shootings, nest tree destruction by city workers, etc.) rather than to some biological inadequacy of the parents. As hatch date followed a normal distribution ( $P > 0.05$ , Kolmogorov–Smirnov tests) we used parametric tests to analyse the relationship between nest-site quality and hatch date (Zar 1984).

We also tested for the repeatability of hatch date and brood size for the same individual birds occupying different nest-sites and for the same nest-sites occupied by different individual birds. This analysis allowed us to quantify the relative effects of a particular female, male and nest-site on these measures of breeding performance (Newton & Marquiss 1984, Zar 1984, Lessells & Boag 1987, Goodburn 1991).

We were also interested in the turnover of individuals at the same nest-sites. Our sample contained a large number of unknown-age females. Therefore, we tested for 'within-individual' changes in the occupation of nest-sites of different quality by comparing nest-site quality for breeding females at their first and subsequent breeding attempts (mean value for subsequent years) by using a paired *t*-test (Zar 1984). For male Merlins we compared nest-site quality within individuals when they were yearlings with that when they were adults (mean value for age 2+) by using a paired *t*-test. Because a large number of male Merlins delay breeding until age 2, we also compared nest-site quality of birds captured when age 2 with that when they were older (mean value for age 3+), again by using a paired *t*-test. In order to conduct a test of whether delayed breeding allowed males to obtain better nest-sites, we compared nest-site

quality for yearling males that bred once to those of 2-year-old males that bred once. We compared these two groups because a previous analysis showed that delayed breeding for males increased their LRS (Espie *et al.* 2000). We used a *t*-test to compare nest-site quality between the two groups (Zar 1984, Siegel & Castellan 1988). As nest-site quality did not follow a normal distribution pattern ( $P < 0.05$ , Kolmogorov–Smirnov test) we used randomization methods for analyses involving this as a dependent variable (Crowley 1992, Adams & Anthony 1996, Manly 1997a).

Birds of any age could be divided into those that bred again in a later year ('lived') and those that did not ('died'). Birds were assumed to have 'died' if they were never recaptured. We used 'died' and 'lived' as categories of the fixed-effect factor in a randomized block ANOVA with age as the blocking factor (Zar 1984, Espie *et al.* 2000). This allowed us to examine within each age group whether any relationship existed between quality of nest-site occupied at a given age and survival to the next age class, i.e. whether birds on poorer nest-sites were more likely to die or simply not return than birds on better nest-sites. We used mean values of nest-site quality in each cell of the block design. We did this because the design was highly unbalanced (i.e. very unequal sample sizes within each category). For analyses involving nest-site quality in the blocked ANOVA, probability levels were determined by randomization methods (Crowley 1992, Adams & Anthony 1996, Manly 1997a). We could not assess any interaction because each cell contained only a single value. Only birds up to age 5 were included in these analyses because our sample contained only one Merlin (a female) older than age 6.

All tests were two-tailed and considered significant when  $P < 0.05$ . All statistical tests were computed using Statistica for Windows (v.6.0) (StatSoft Inc. 1995). Randomization tests were conducted using the computer program RT (v.2.1) (Manly 1997b). If the number of permutations for reshuffling and sampling the data were small ( $< 2000$ ) we used exact permutation to calculate probability values. If the number of permutations was large, we performed 5000 replications and used the frequency distribution of possible outcomes to calculate probability values (see Crowley 1992, Adams & Anthony 1996, Manly 1997a). Probability values calculated from randomization techniques are denoted as  $P_r$ . Results given below are reported as means  $\pm 1$  sd unless otherwise indicated.

## RESULTS

We identified 59 separate nest-sites that were used between 1985 and 1995 on which nesting occurred 308 times. However, not all nest-sites were occupied in a given year. The mean occupancy rate for nest-sites was 5.2 (sd =  $\pm 3.4$ ) years and the range was 1–11 years.

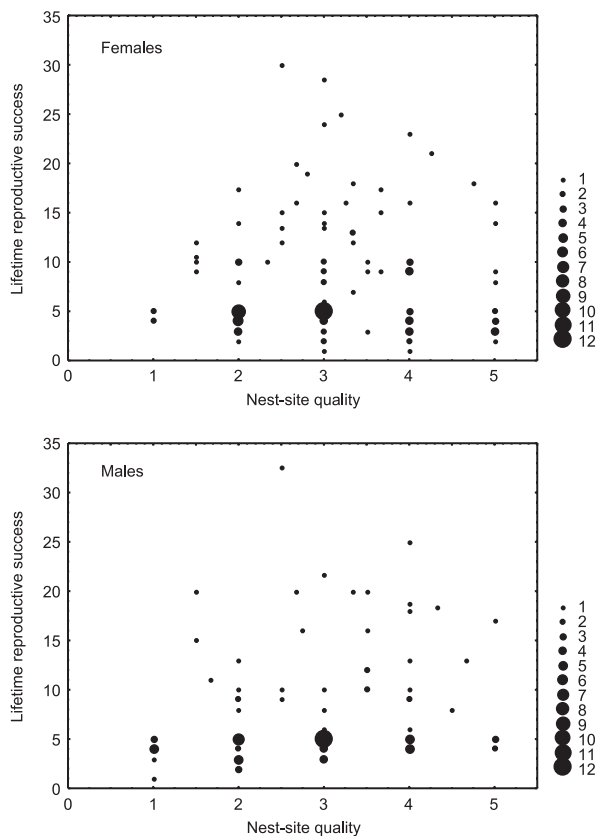
### Effects of nest-site quality

Female Merlins that switched nest-sites occupied higher quality nest-sites on subsequent breeding attempts (3.17 (sd =  $\pm 1.07$ )) than they did when breeding for the first time (2.73 (sd =  $\pm 1.29$ );  $t = 1.73$ ,  $n = 42$ ,  $P_r = 0.0448$ ). For males that switched nest-sites there was little difference in quality between age 1 (3.13 (sd =  $\pm 1.46$ )) and age 2 + (2.88 (sd =  $\pm 1.13$ );  $t = 0.39$ ,  $n = 8$ ,  $P_r = 0.72$ ), but a substantial difference between age 2 (2.33 (sd =  $\pm 0.87$ )) and age 3 + (3.22 (sd =  $\pm 1.12$ );  $t = 1.92$ ,  $n = 9$ ,  $P_r = 0.0586$ ). It is also noteworthy that Merlins that bred initially at nest-sites of rank 1 never switched to nest-sites of rank 1 in a subsequent breeding attempt. Males that delayed breeding until age 2 (and only bred once) did not occupy better nest-sites (median = 3.0,  $n = 46$ ) than yearling males that only bred once (median = 3.0,  $n = 13$ ; Mann–Whitney  $U = 281.5$ ,  $P = 0.74$ ). Nest-site quality was not correlated with lifetime reproductive success in females ( $T = -0.028$ ,  $n = 127$ ,  $P = 0.636$ ), but in males the two were positively correlated ( $T = 0.205$ ,  $n = 98$ ,  $P = 0.0027$ ; Fig. 1).

Using analysis of variance blocked by age we found that female Merlins that survived past each age category had not occupied nest-sites of different quality from those of females that had died ( $F_{1,4} = 0.54$ ,  $P_r = 0.25$ ; Fig. 2). Among males, however, birds surviving past each age category did occupy better quality nest-sites than those same-aged males that were not recaptured ( $F_{1,4} = 5.93$ ,  $P_r = 0.03125$ ; Fig. 2). For the same nest-sites occupied by different females, neither hatch date ( $r = 0.020$ ,  $F_{47,131} = 1.08$ ,  $P = 0.361$ ) nor brood size ( $r = 0.065$ ,  $F_{46,133} = 1.26$ ,  $P = 0.154$ ) was repeatable. Hatch date ( $r = 0.119$ ,  $F_{37,66} = 1.37$ ,  $P = 0.132$ ) and brood size ( $r = -0.061$ ,  $F_{37,66} = 0.84$ ,  $P = 0.709$ ) were also not repeatable for the same nest-sites occupied by different males.

### Effects of individual quality

For the same females occupying different nest-sites over their lifetimes, both hatch date ( $r = 0.381$ ,

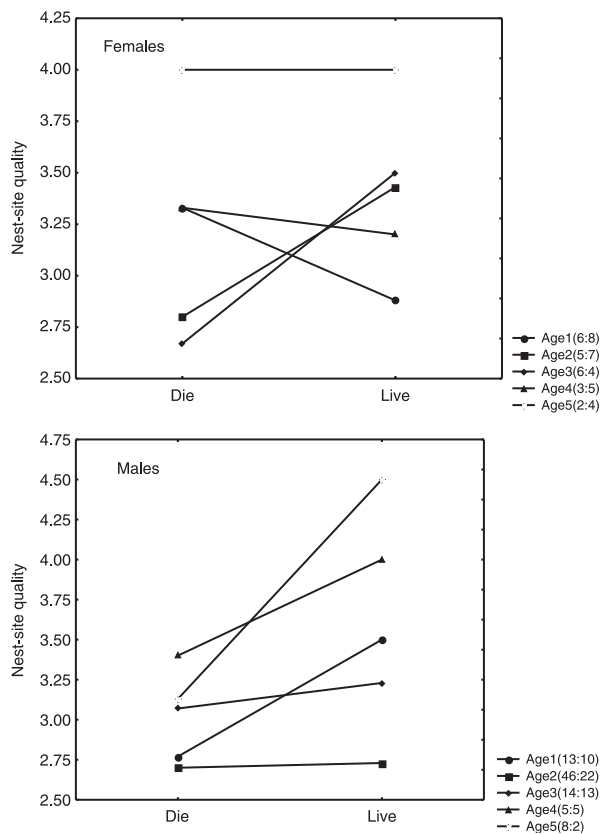


**Figure 1.** Lifetime reproductive success and average quality of territory occupied for Merlins breeding in Saskatoon 1985–95. Kendall's tau correlation revealed a positive relationship between the two variables for male Merlins but not for females.

$F_{45,66} = 2.50$ ,  $P < 0.001$ ) and brood size ( $r = 0.228$ ,  $F_{46,67} = 1.72$ ,  $P = 0.022$ ) were repeatable. However, among individual males occupying different nest-sites, hatch date ( $r = 0.060$ ,  $F_{19,23} = 1.37$ ,  $P = 0.38$ ) and brood size ( $r = 0.258$ ,  $F_{19,23} = 1.74$ ,  $P = 0.102$ ) were not repeatable.

## DISCUSSION

Tradeoffs between fitness components are inevitable from a life history perspective and evidence from brood size manipulation studies in birds suggests that increased reproductive effort may affect future fecundity and survival (reviews in Lessells 1991, Roff 1992, Stearns 1992). However, some non-experimental field studies report a positive relationship between current reproduction and survival (Smith 1981, Safriel *et al.* 1984, Coulson & Porter 1985, Espie *et al.* 2000). van Noordwijk and de Jong (1986) posit that this positive relationship may



**Figure 2.** Mean nest-site quality for Merlins in Saskatoon that survived past, or died (i.e. never returned) at, a particular age. Two-factor randomized block ANOVA tests (blocked for age effects) revealed an overall difference in territory quality for surviving vs. dead males but not for females. Connecting lines are used to illustrate equal-aged birds. Numbers in the key indicate sample sizes for each category (die : live).

result from variation in the resources available to different individuals. Alternatively, it may be related to the quality (Coulson & Porter 1985, Coulson & Thomas 1985, Goodburn 1991) of the individuals concerned, or to the quality of nest-sites occupied (Newton 1991, Ens *et al.* 1992, Valkama & Korpimäki 1999). Our study of male and female Merlins provides evidence that bird quality, and to a lesser extent nest-site quality, influences reproduction in a natural population. This work also reinforces the idea that these factors may act in combination to influence breeding performance.

## Influence of nest-site quality on breeding performance in Merlins

There is a large body of evidence showing that habitat quality can influence the breeding performance

of birds in general (reviews in Ens *et al.* 1992, Rodenhouse *et al.* 1997, Newton 1998), and raptors in particular (Korpimäki 1989, Newton 1991, Franklin *et al.* 2000). Merlin occupation of nest-sites was non-random and there are good data to show that Merlins in Saskatoon select a subset of nest-sites from a larger number of possible nest-sites that remained unused (Warkentin & James 1988). Except for a few specific circumstances (e.g. Viitala *et al.* 1995), little is known about how raptors and other birds may assess territory quality. Some studies have shown that poor breeding performance in one year can lead to a change of breeding territory in the next (Newton & Marquiss 1982, Shields 1984, Sonerud 1985, Beletsky & Orians 1991, Korpimäki 1993, Newton 1993, Wiklund 1996). Nevertheless, some avian species return in successive years to breed in the same territories or nest-sites despite failure (Haig & Oring 1988). Birds that breed in the same area may benefit from previous experience in terms of obtaining food and mates, territory defence and evasion of predators (Greenwood & Harvey 1982, Moore & Ali 1984, Shields 1984, Dobson & Jones 1986). Site fidelity is higher among male than female Merlins (Warkentin *et al.* 1991, Wiklund 1996), and female raptors in general tend to disperse further than males (Newton 1979, 1986, Village 1990, Korpimäki 1993). Mate fidelity is low among Merlins in the Saskatoon population (20% of pairings contained the same birds for two consecutive years; Warkentin *et al.* 1991) and appears largely to be related to the degree of site fidelity. Whereas site fidelity has been shown to make a difference in some species, there is no apparent reproductive benefit of site fidelity to Merlins in Saskatoon (Warkentin *et al.* 1991).

Our results from this study indicate weak links between nest-site quality and female Merlin productivity, timing of breeding and survival. Furthermore, neither hatch date nor brood size was repeatable for nest-sites occupied by different females. Even so, when female Merlins switched nest-sites they tended to settle the next year in areas of higher quality. Thus, female Merlins in Saskatoon apparently use some cues to assess nest-site quality; however, these features do not appear necessarily to enhance their breeding performance.

For male Merlins, nest-site quality did have a positive association with lifetime reproductive success but showed little or no association with the other measures of breeding performance. Nonetheless, when male Merlins switched nest-sites they also tended to move to ones of higher rank. In addition,

male Merlins surviving past each age category occupied nest-sites of higher quality; hence, annual survival (or at least returning to breed again) may have been associated with nest-site quality and this in turn may have resulted in higher LRS for these individuals. Nevertheless, neither hatch date nor brood size for different males occupying the same nest-sites was significantly repeatable. Thus, the influence of nest-site quality on male Merlins in Saskatoon was more extensive than for females, but was still quite limited.

Males that delayed breeding for a year did not obtain higher quality nest-sites than males that bred as yearlings. This is an important finding because other work on birds has shown that delayed breeding allows individuals to obtain higher quality territories in some species (Stacey & Ligon 1987, Zack 1990, Koenig *et al.* 1992, review in Zack & Stutchbury 1992). Other work on Merlins (Espie *et al.* 2000) has shown that a delay of breeding for 2-year-old males increased their LRS over those males that bred as yearlings. From our two studies, it seems that some male Merlins delay breeding to improve skills (and thereby enhance their LRS) rather than to obtain better nest-sites and increase productivity.

Perhaps the absence of general trends in how habitat heterogeneity influences breeding performance in the Saskatoon Merlin population may be related to the unique features of the species, the study area or a combination of these two factors. Merlins do not build their own nests and so are limited to nesting in areas where corvids (American Crows and Black-billed Magpies *Pica pica*) have already built nests in the city (Sodhi *et al.* 1993). The criteria on which corvids select nest-sites probably differ from those used by Merlins, but the result is that Merlins are restricted to areas of the city that corvids prefer for breeding (almost exclusively residential areas as opposed to industrial or commercial areas). In addition, House Sparrows act as the predominant prey of Merlins in Saskatoon (Sodhi & Oliphant 1993) and Sparrows occur at higher densities in the city and in industrial areas (e.g. grain elevators, seed mills, rail yards) than they do outside the city or in residential areas. Thus, the Merlin's primary food source is available in abundance, but not in quantities or locations that might be defended. In Saskatoon, hunting ranges of radiotagged males overlap spatially by up to 77% (Sodhi & Oliphant 1992). These authors thus concluded that Merlins have non-exclusive hunting ranges for at least three reasons: (1) the high density of Merlins nesting in the city may make defence

costly; (2) the prey base is abundant, widespread and stable in Saskatoon so there are few benefits to exclusive ranges; and (3) the prey (small birds) are hard to defend because they are mobile and alert to the presence of Merlins. Therefore, the abundance, accessibility and mobility of food in the city may negate some advantages of occupying a specific nest-site to breed.

### **Influence of bird quality on breeding performance**

The concept of individual quality was introduced by Coulson (1968) to emphasize the fact that not all individuals are equal. For Merlins we assessed bird quality through the repeatability of breeding performance (hatch date and brood size) for the same birds occupying different nest-sites (van Noordwijk *et al.* 1980, Newton & Marquiss 1984, Goodburn 1991, Hochachka 1993). For Merlins in Saskatoon, it appears that time of breeding and the size of the brood are largely determined by the female. For males, the two measures of breeding performance were not statistically repeatable. This finding differs from that for Eurasian Sparrowhawks *Accipiter nisus*, in which the repeatability of laying date was greater for males than for females (Newton & Marquiss 1984, Lessells & Boag 1987). Indeed, much of the reproductive potential of a female raptor is likely to be a function of the quality of her mate, which will provide food for the breeding attempt (Newton 1979, 1986, 1988, Wijnandts 1984, Village 1990). Why then were hatch date and brood size not repeatable for male Merlins? It is thought that, when individuals do not display repeatable performance, there may be non-random variation in quality within individuals (Hochachka 1993). For instance, in male Merlins breeding performance has been shown to improve with age, probably as a consequence of improved foraging skills through increased experience (Espie *et al.* 2000), and this may have reduced repeatability. Moreover, birds should not repeat the conditions that caused the previous failure of reproduction (Hochachka 1993). This last idea probably has little bearing on our study because all birds examined had produced at least one chick and complete failure at nests was uncommon (Sodhi *et al.* 1992). Nonetheless, in our Saskatoon Merlin population females appear to have ultimate control over breeding.

Another possibility is that males in Saskatoon adjusted their hunting effort to fit the situation at hand

(Sodhi 1993). Food abundance directly influences body reserves stored by adult raptors, as well as their breeding performance (Drent & Daan 1980, Dijkstra *et al.* 1982, Newton *et al.* 1983, Martin 1987, Korpimäki 1989, Chastel *et al.* 1995, Wiehn & Korpimäki 1997). In Saskatoon, Merlins time their breeding so that the fledging phase of their chicks falls during the time of peak production of juvenile House Sparrows (Sodhi *et al.* 1992, Sodhi & Oliphant 1993), thereby enabling them to exploit this particularly vulnerable food supply whilst maintaining their own body reserves. Other workers have reported increased predation on juvenile prey as the Merlin breeding season progresses (Newton *et al.* 1984). Because male Merlins provide almost all the food for themselves, their mate and their offspring during the breeding season (Sodhi *et al.* 1992), one would expect a male's ability to provide food to be the primary determinant of breeding success. Merlins, like other raptors, are unusual among birds in that males appear to invest substantially more energy in offspring than do females (Wijnandts 1984, Masman *et al.* 1988). Moreover, for bird-eating raptors the breeding attempt hinges on the ability of the male to provide food (Newton 1986, 1988, Aparicio & Bonal 2002). In their supplemental feeding experiment, Wiehn and Korpimäki (1997) found that male Common Kestrels *Falco tinnunculus* did not adjust their parental effort within a season and they suggest that male parental effort is fixed at a level at which survival is not jeopardized. In Merlins, hunting effort is not fixed. It is highest during the nestling phase and is related to brood size so that males with larger broods show increased foraging (Sodhi 1993). In addition, those males on higher quality territories may have gained a slightly better chance of survival through reduced hunting effort. Sodhi (1993) showed that males with high prey abundance in their hunting ranges spent less time flying than males with low prey abundance in their hunting ranges. Perhaps some high-quality nest-sites allowed for slightly improved access with less energy expenditure to areas of higher prey abundance within the city. Future work on Merlins should focus on determining in greater detail why certain nest-sites are more desirable than others.

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