#### THE INFLUENCE OF

# RELATEDNESS, WEIGHT, AND AGE ON THE MATE CHOICE OF

#### CAPTIVE FEMALE AMERICAN KESTRELS

A Thesis

by

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Submitted to the Faculty of Graduate Ludies and Research

in partial fulfillment of the requirements

for the degree of

Master of Science

Wildlife Resources,

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C March 1985

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Suggested Short Title:

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Mate Choice in Captive Female American Kestrels

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#### ASSTRACT

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Renewable Resources (Wildlife)

#### THE INFLUENCE OF

RELATEDNESS, WEIGHT, AND AGE ON THE MATE CHOICE OF CAPTIVE FEMALE AMERICAN KESTRELS

High male parental investment is essential to reproductive success in raptors. However, genetic inheritance must also figure strongly and may therefore be a basis for mate choice. Female American kestrels (Falco sparverius) were given the opportunity to chose between two males differing with respect to relatedness, weight, or age. Siblings and smaller males were not chosen in significantly (P>0.05) different frequencies than if females had done so at random. Significantly (P<0.05) more females chose two-year old males with breeding experience than old inexperienced males. , American one-year kestrels are infrequently philopatric and the scarcity of suitable nesting cavities limits their breeding densities. Thus there may be little selection pressure for incest avoidance by means of kin recognition. Reversed size dimorphism in kestrels is more likely due to environmental pressures or intrasexual competition than to sexual selection via mate choice. However, generalized indicators of male fitness (e.g. age) may play a role in the choice of mates.

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#### J.R. Duncan

L'Influence de la Warenté, du Poids et de l'Age sur le Choix d'un Partenaire Sexuel Chez les Femelles de la Crécerelle d'Amérique en Captivité.

Résumé

Chez les oiseaux de proie, un investisement reproductif élevé est requis du mâle. Cependant, l'hérédité génétique doit aussi figurer de façon prononcée et pourrait donc servir dans le choix d'un partenaire sexuel, Des femelles de la crécerelle d'Amérique (Falco sparverius) eurent l'occasion de choisir entre deux mâles de l'espèce différant quant à leur degré de parenté, leur poids, ou leur âge. Les frères et les mâles pesant relativement peu furent choisis au hazard (P>0.05) tandis que les mâles âgés de deux ans et expérimentés à la reproduction furent préférés à ceux ayant un an seulement et n'ayant aucune expérience reproductive (P(0.05). Les crécerclles d'amérique sont peu philopatriques et les pénuries de cavités convenant à la reproduction peuvent limiter leur densité sur les aires de reproduction. Ainsi, il se pourrait qu'il y ait peu de pression sélective pour énviter l'inceste au moyen de reconnaissance des individus parents. Le dimorphisme sexuel renversé chez les crécerelles serait le résultat de pressions environmentales ou de compétition intrasexuelle plutôt que le résultat de

sélection sexuelle via le choix de partenaires. Toutefois, des indicateurs généraux de la qualité du mâle (e.g. âge) pourraient jouer un rôle dans le choix de partenaires sexuels.

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### ACKNOWLEDGEMENTS

I would like to thank Kelly Brock, Jean Cypher, Sylvie Drouin, André Lavigne, Ron Meyers, Ian Ritchie, and Laird Shutt for their technical assistance.

I wish to express my gratitude to J. Cypher and to Drs. J.R. Bider, D.M. Bird, G.J. Doucet, P. Laguë, and R.D. Titman for their meticulous scrutiny of various drafts of the manuscript. I am particularly grateful to Dr. Bird who proposed this study and introduced me to raptor research.

I wish to thank the Natural Sciences and Engineering Research Council of Canada and La Ministère du Loisir, de la Chasse, et de la Pêche du Québec for their financial assistance to Dr. Bird which made this study possible. Personal financial support (1984) from the Department of Renewable Resources was appreciated.

A special thanks goes to my parents, James and Constance Duncan, for their enduring support and encouragement.

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#### PREFACE

In the last few years, various avian species have been used in experiments to test the influence of male genetic quality on female mate choice. In such tests researchers hold constant confounding factors such as intrasexual competition and offer females a choice between males that differ in only one trait. One prerequisite however, is a sample of birds whose values for the characteristic under investigation are known. For example, studies involving preferences for relatedness require either pedigreed colonies of captive-bred species (Bateson 1983; Ratcliffe 1983) or marked wild populations that have been studied over several generations (Greenwood <u>et al</u>. 1979; Koenig & Pitelka 1979; van Noordwijk & Scharloo 1981). The Macdonald Raptor Research Centre of McGill University maintains a pedigreed colony of American kestrels (<u>Falco</u> <u>sparverius</u>), and so provided an excellent opportunity to investigate the influence of relatedness, weight, and age on mate choice by females.

Experimental designs in which birds were not permitted to interact (Bateson 1983), or studies of short duration (Burley & Moran 1979), could provide biased results since "a female may express different choices at different times, according to her physiological state" (Halliday 1983). The tests described herein were designed so that the birds could interact continuously for five days and observation sequences were randomized.

As permitted by the Faculty of Graduate Studies, this thesis includes the text of a manuscript to be submitted to the journal <u>Animal Behaviour</u> for publication with Dr. D.M. Bird as co-author. Data collection and analysis were conducted independently by this author. References, tables, and figures appear after the manuscript, and the style adopted is that of the journal to which the manuscript will be submitted.

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The following is included in accordance with the regulations of the McGill University Faculty of Graduate Studies.

"The Candidate has the option subject to the approval of the Department, of including as part of the thesis the text of an original paper, or papers, suitable for submission to learned journals for publication. In this case the thesis must still conform to all other requirements explained in this document, and additional material (e.g. experimental data, details of experiment and experimental design) may need to be provided. In any case abstract, full introduction and conclusion must be included, and where more than one manuscript appears, connecting texts and common abstract, introduction and conclusions are required. A mere collection of manuscripts is not acceptable; nor can reprints of published papers be accepted.

While the inclusion of manuscripts co-authored by the Candidate and others is not prohibited for a test period, the Candidate is warned to make an explicit statement on who contributed to such work and to what extent. Copyright clearance from the co-author or co-authors must be included when the thesis is submitted. Supervisors and others will have to bear witness to the accuracy of such claims before the Oral Committee. It should also be noted that the task of the Exterminal Examiner is much more difficult in such cases,"

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RELATEDNESS, WEIGHT, AND AGE ON THE MATE CHOICE OF

CAPTIVE FEMALE AMERICAN KESTREES

#### ABSTRACT

High male parental investment is essential to reproductive success in raptors. However, genetic inheritance must also figure strongly and may therefore be a basis for mate choice. Female American kestrels (Falco sparverius) were given the opportunity to chose between two males differing with respect to relatedness, weight, or age. Siblings and smaller males were not chosen in significantly (P>0.05) different frequencies than if females had done so at random. Significantly (P<0.05) more females chose two-year old males with breeding experience old inexperienced males. than one-vear American kestrels are infrequently philopatric and the scarcity of suitable nesting cavities limits their breeding densities. Thus there may be little selection pressure for incest avoidance by means of kin recognition. Reversed size dimorphism in kestrels is more likely due to environmental pressures or intrasexual competition than to sexual selection via mate choice. However, generalized indicators of male fitness (e.g. age) may play a role in the choice of mates.

#### Introduction

The primary goal of mate choice studies has been to demonstrate that natural selection favours mechanisms enabling individuals to choose mates of the highest quality. Selection pressures have operated in a variety of ways on different species to produce a continuum of discriminatory abilities. These range from indiscriminate mass spawnings of certain fish (Bond 1979) to finely-tuned choice mechanisms involving genotypes, such as kin recognition (Bateson 1983). Not surprisingly, investigators have revealed a variety of cues used by organisms to choose mates. Grant & Colgan (1983) discussed factors influencing female choice including resources provided (e.g. courtship feeding (Nisbet 1973)), and defended (e.g. nesting sites (Pleszczynska 1978; Garson 1980)) by the male. These factors reflect aspects of male quality directly affecting the female's fitness.

In contrast, phenotypic markers of genetic quality may affect her offspring's fitness (Howard 1978). Examples include body size (Hanson & Smith 1967; McCauley & Wade 1978), relatedness (Bateson 1982), and age (Burley & Moran 1979). The influence of these above three criteria on the mate choices of captive female American kestrels (<u>Falco sparverius</u>) was investigated. Research was facilitated by the availablity of a large pedigreed colony maintained at the Macdonald Raptor Research Centre of McGill University (Bird 1982). This species breeds readily in captivity and is sexually mature in its first spring.

Halliday (1983) defines mate choice as "any pattern of behaviour, shown by members of one sex, that leads to their being more likely to

mate with certain members of the opposite sex than with others." Behaviours indicative of American kestrel pair-bond formation during the pre-nesting period have been well documented (Willoughby & Cade 1964; Balgooyen 1976) and are readily exhibited in captivity (Willoughby & Cade 1964; Dlendorff 1968). That this study investigated the choice of males by females does not imply that males do not discriminate. However, to ensure sufficiently large sample sizes this restriction was necessary.

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#### Methods

description of the annual maintenance and captive A breeding procedures for the McGill kestrel colony is provided by Bird (1982). In the 1983 and 1984 breeding seasons, a cumulative total of 35 sexually mature females from 22 clutches was studied. Nine siblings. including four females. from four clutches had been separated and reared apart by foster-parents. The remaining 31 females had been reared with their siblings by their natural parents. In the fall the birds were overwintered unisexually in flight pens measuring 7.5 x 6.5 x 2.5 m (L x W x H), each containing up to 30 individuals. Birds were maintained on day-old cockerels supplemented every two days with dietary limestone or with SA-37 (Rogar-STB Division of BTI Products, Inc., Montreal, Quèbec) vitamin/mineral supplements every other day. All birds were kept on natural photoperiod.

Weight and relatedness choices were tested simultaneously. From April 25 to May 17, 1983, and from April 9 to May 2, 1984, females were given the opportunity to choose between a male sibling and a non-related strange male of the same age and breeding experience. Each female was tested once with each of her male siblings yielding a total of 50 tests. Non-related males had a coancestry coefficient less than 0.02 with respect to the test female (Pirchner 1983). From April 24 to May 12, 1984, nine two-year old females with breeding experience were given a choice between two non-related strange males: a two-year old with breeding experience and an inexperienced one-year old.

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#### Apparatus

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Mate choices were determined in isolated test-pens (Fig. 1) measuring 2.5 x 1.5 x 2.5 m (L x W x H), each consisting of an opaque polyethylene divider resting on a masonite platform (Bird & Goldblatt 1981). On either side of the divider was a wooden nest-box with shavings and a wooden perch to which a male was tethered in a modified falconer's fashion. Males had access to their nest-boxes, but were visually isolated from each other. A wooden T-perch was attached to the edge of the platform extending far enough to give the free-flying female a view of both tethered males simultaneously. The birds were observed through one-way mirrors (30 x 5 cm) located in the door of each pen.

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Test Schedule

Over a test period lasting eight days, males were tethered in place on day one and were-allowed to acclimate for two days. Observations began at least one hour after the introduction of test females on the morning day three. Each pen was observed for three 20 minute intervals per of morning, noon and afternoon, for five days. The sequence in which day: pens were observed was random. The male's position within each pen the switched half-way through the observation period to ensure that a was female was not choosing a side as opposed to a male. Each day birds were fed day-old cockerels ad libitum before the morning observation interval. All birds were weighed twice, before feeding, on the mornings of days three and eight. A bird was placed in a felt bag and weighed with a Pesola 200 g spring scale to the nearest gram. After recording weights on day eight, the birds were either returned to the

flight pens and maintained unisexually, or relocated for the next test period. No birds used more than once were tested in the same pen twice. All observations were recorded by the first author for the weight and relatedness tests, however a trained assistant helped for the age tests in 1984.

#### Choice Criteria

The four criteria described below vary in their relative strength as indicators of American kestrel pair-bond formation during the prenesting period (Willoughby & Cade 1964; Balgooyen 1976). The values of all criteria were compared before and after the males' positions were switched to score the test females as having chosen a mate, chosen a side, or having made no choice.

1.Location of the female: American kestrels are quite sociable in the pre-nesting period, often perching in contact with each other. This criterion was summarized as a percentage of the total observed time spent by a female with either one of the males or in a neutral area. She was considered to be interested in a male when she remained within his reach for at least one minute.

2.Nest-box Inspections: The direction of attention and activity toward the nest-site is important in establishing an attachment of the mates to a mutually acceptable nest and in stimulating the birds sexually (Willoughby & Cade 1964). The female inspected a nest-box when she entered it or perched at its entrance with her head and shoulders inside. The frequency of this behaviour was recorded.

3.Copulations: Female American kestrels solicit copulations with potential mates early in the pre-nesting period by leaning forward with the tail held at a 45 degree angle (Willoughby & Cade 1964). The mounting of the female by a male, together with subsequent copulatory movements, was recorded as a copulation. Unsuccessful attempts of the males to mount unsoliciting females were not recorded.

4.Food-transfers: Courtship feeding functions to maintain previously established pair-bonds in most monogamous species (Nisbet 1973). A successful food-transfer was recorded if a female accepted food from a displaying male (Willoughby & Cade 1964).

These behaviours, indicative of pair-bond formation, have been well documented (Willoughby & Cade 1964; Balgooyen 1976) and are readily exhibited in captivity (Willoughby & Cade 1964; Olendorff 1968). However, females are sometimes promiscuous early in the breeding season (Willoughby & Cade 1964). Promiscuity was observed during the tests (Table 1), but the trend indicates, as Willoughby & Cade (1964) stated. that food transfers are fairly consistent indicators of strong pair bonds. These occurred too infrequently (Table 1) to use as a sole Therefore, a female was criterion for determining mate choices. considered to have chosen a male if she received food-transfers from him and/or copulated more frequently with him both before and after his position was switched as previously described. She was recorded as having made no choice if no copulations or food-transfers were observed. Nest-box inspection frequency and the location of the female were used

when necessary to resolve small frequency differences or inconsistencies in the copulation and food-transfer criteria. All four criteria were used to ensure that females were not choosing sides as opposed to males. If she interacted more frequently with a different male after they were switched, she was recorded as having chosen a side. Tests in which a female made no choice or chose a side were not included in the analysis.

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To determine whether early nestling experience or weight influenced the proportion of females that chose siblings, the Fisher Exact Probability Test (Daniel 1978) was used. The one-tailed Binomial Test (Daniel 1978) was employed to detect if females chose older males significantly more often than if they had done so at random. Due to a sufficiently large sample size the one-tailed Normal Approximation to the Binomial (Ostle & Mensing 1975) was used to resolve whether females chose either non-siblings or lighter males significantly more often than if they had done so at random. The One-Sample Runs Test (Daniel 1978) . was used to determine whether relative weight preferences were randomly distributed as the absolute weight differences between males increased. "The level of significance was 0.05 for all the above tests.

#### Results

When analyzed separately for each year, the data yielded consistent results and was therefore pooled. In 50 tests, 33 females made a choice, nine made no choice, and eight chose a side.

#### (1) Mate Choice: Siblings vs. Strangers.

(a) Familiarity: There was no significant difference (P=0.558; Fisher Exact Probability Test) in the proportion of females that chose brothers for those birds reared together with their siblings and those raised apart (Table II).

(b) Relatedness: More females chose unrelated males than their siblings (Table II), but the trend was not significantly different than if males were chosen at random (P=0.149; One-tailed Normal Approximation to the Binomial).

(c) Weight: There were 28 tests where a female made a choice and the average weight difference between the two choice males was at least two grams. The proportion of females that chose brothers which were the heavier or lighter of the two males offered (Table III) was not significantly different from that of those who chose non-related males (P=0.167; Fisher Exact Probability Test). More females chose the lighter of the two males offered (Table III), but not significantly more than if they had done so at random (P=0.284; One-tailed Normal Approximation to the Binomial). Absolute average weight differences between pairs of choice males ranged from 2 to 30 grams and when arranged in increasing order, the sequence of the average versus lighter male choice was random (P>0.05; One-sample Runs Test).

(2) Mate Choice: Age.

In nine tests seven females chose a two-year old male, one chose a one-year old male, and one made no choice. The proportion of females

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choosing two-year old males was significantly greater than if males were chosen at random (P=0.032; One-tailed Binomial).

#### Discussion

#### Relatedness

The optimal outbreeding hypothesis, as elaborated by Bateson (1983), predicts that individuals should avoid choosing siblings as mates due to the genetic costs. Inbreeding costs are also known as inbreeding depression or a decrease in the mean level of characters related to fitness, such as reduced fertility or hatchability (Falconer 1982). Recent studies have shown that many avian (Koenig & Pitelka 1979; Bateson 1982; Ratcliffe 1983) and mammalian (Dewsbury 1982; Hoogland 1982; Duncan et al. 1984; Gayish et al. 1984) species demonstrate. behavioural discrimination against siblings when choosing mates. This ability requires the organism to assess the degree of relatedness of its potential suitors. Mechanisms of kin recognition, as reviewed by Blaustein (1983) and Holmes & Sherman (1983), may be based on the familiarity of conspecifics (Bateson 1983; Gavish et al. 1984), or on a genetic component (Hepper 1983), such as phenotypic matching or recognition alleles. American kestrels apparently lack such a mechanism or at least did not employ it to avoid incestuous sibling mate choices. Holmes & Sherman (1983) believe that mechanisms of kin recognition are selected under rare conditions. They state " Dispersal and mortality are the crucial demographic parameters, because kin selection will have acted only on those categories of relatives that have consistently

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coexisted in proximity to one another across evolutionary time, so that social interactions have regularly occurred between them."

Henny (1972) estimates that American kestrels suffer high mortality, both as adults (47%) and as juveniles (69%). They appear to be infrequently philopatric (Bowman <u>et al</u>. 1985) and a scarcity of suitable nest cavities limits their breeding densities (Hamerstrom <u>et al</u>. 1973). Thus American kestrels have probably experienced little, if any, selection pressure to develop a mechanism of kin recognition to avoid incest. That early nestling experience had no effect on subsequent choices is therefore not surprising. Bowman <u>et al</u>. (1985) report that of 271 wild American kestrels banded over four years at Ste. Anne de Bellevue, Québec, only one juvenile, returning to its natal area, committed incest by breeding with its father.

Long-term population studies of the great tit (<u>Parus major</u>) revealed a lack of behavioural incest avoidance for this species as well. Adverse inbreeding effects in an island population were offset by higher recruitment of young from nests where at least one parent was inbred (Noordwijk & Scharloo 1981). A second population was thought to avoid inbreeding costs via a differential dispersal pattern for male and female young (Greenwood 1979). However, Moore & Ali (1984) point out that a large percentage of the individuals in Greenwood's study are still at risk since "statistical differences in the average distance dispersed by each sex do not affect most individuals." Although the frequency of incest may be somewhat reduced by differential dispersal of young organisms, incest avoidance is not necessarily the driving force. Moore & Ali (1984) maintain that incest avoidance via sexual dispersal patterns are epiphenomenal consequences of intrasexual competition and territory choice. Cases where young peregrine (<u>F. peregrinus</u>) and prairie falcons (<u>F. mexicanus</u>) were driven away from their natal cliffs the following spring by their parents are known (Newton 1979).

Newton & Marquiss (1982), in a study on the fidelity to breeding area and mate in sparrowhawks (<u>Accipiter nisus</u>), found that yearlings move more frequently and farther than older birds. Additionally, they observed that males exhibited greater residency than females. The movement patterns of this non-migratory raptor species are not necessarily due to fidelity to mate or nest site, but are expressed in response to food resources and territory quality (Newton & Marquiss 1982). As information on the paternity of the birds was not available, possible incestuous pairings could not be detected.

A long-term, marked population study on American kestrels is necessary to determine the frequency and occurrence of inbreeding under natural conditions.

Weight

Most birds of prey exhibit reversed size dimorphism, the female being larger than the male. Earhart & Johnson (1970) noted that weight is the best indicator of overall body size. The American kestrel weighs from 85

to 140 grams, the female averaging slightly larger and heavier than the male (Bent 1938; Willoughby & Cade 1964). Johnson (1978) and Newton (1979) review many explanations for this phenomenon in raptors. Newton regards the link with feeding habits as the `ultimate' cause. The male's smaller size may allow him to specialize on smaller, more numerous prey species enabling him to more easily support both himself and his family's growing needs during the breeding season (Storer 1966; Reynolds 1972).

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Among the 'proximate' causes are explanations with a behavioural basis such as the necessity of larger female size and dominance for the successful reproduction of these inherently aggressive birds (Cade 1960; Amadon 1975). That female American kestrels chose the larger of the two males almost as frequently as the smaller casts some doubt on the above explanation. Furthermore, Willoughby & Cade (1964) found no reduction in the reproductive success of captive kestrel pairs in which the females were one third smaller than the males.

While male birds of prey provide food for their mates and young during most of the breeding season (Newton 1979), it is unlikely that females have to force them to surrender it. Unusual food transfers whereby a female provided a food item to the male for subsequent transfer to her was observed twice in this study and in wild kestrels, too (Bird & Spiegel 1975). Smith (1982) noted that "courtship feeding is a male's most direct way to contribute to his own egg's (and young's) quality."

Our data seem to support Newton's (1979) contention that female dominance is more likely a consequence of reversed size dimorphism and not the underlying cause.

Age

American kestrels readily breed in their first spring (Bent 1938). However, few individuals survive to successive breeding seasons due to high annual mortality (Henny 1972). Thus age, as a mate choice criterion, can be considered a generalized indicator of male fitness. In this study seven of eight females chose a two-year old male over a oneyear old (Table III). Similar age preferences were demonstrated for the black-capped chickadee (<u>Parus atricapillus</u>) by Howitz (1984). Burley and Moran (1979) determined that female pigeons (<u>Columbá livia</u>) preferred males with breeding experience over inexperienced birds. Since the twoyear old males used in our study had previous breeding experience whereas the one-year olds did not, we cannot separate the relative influences of age and experience.

Experience may also affect other abilities necessary for successful reproduction (e.g. male hunting skills). American kestrels, and other raptors, depend on the male's ability to catch enough prey to support the pair and their young for most of the breeding season (Bent 1938). Reynolds (1972) stated "The fact that immature accipiter males do not breed, whereas immature females do, may indicate the importance of experience in increasing the foraging efficiency of the male." Webster (1944) observed juvenile female prairie falcons successfully raising families, but he never saw juvenile males do this. Female common terms (<u>Sterna hirundo</u>) may assess the hunting abilities of males by the amount of food offered, since this affects the pair's reproductive success (Nisbet 1973). Wild American kestrel females may use a similar criterion, but the captive birds used in this study were fed <u>ad libitum</u>. Thus our males had no shortage of food to display, which they did frequently while hopping in and out of their nest boxes.

Plumage was the most obvious difference between one and two-year old males. First year males possessed variably streaked pale underparts, while older birds had few, if any, streaks, and a darker reddish-brown chest. Captive American kestrels, along with accipiters (<u>Accipiter</u> spp.) and harriers (<u>Circus</u> spp.), exhibit eye-colour changes with age long after the definitive plumage is acquired (D.M. Bird, unpubl. data; Snyder & Snyder 1974; Balfour 1970, respectively). These differences may provide females with badges for age identification and discrimination when choosing mates. It may be advantageous for females to choose older males who are more likely to be better at providing the female and her young with adequate food resources for successful reproduction.

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Age discrimination may play another important role since female American kestrels are sometimes promiscuous early in the nesting season (Willoughby & Cade 1964). Once a pair is established on a territory, the female is occasionally promiscuous with neighbouring males (Willoughby & Cade 1964). A study on red-winged blackbirds (<u>Agelaius</u> phoeniceus) showed that neighbouring males often sired the young of

females within a vasectomized males' territory (Bray <u>et al</u>. 1975). It would increase the genetic fitness of a female's offspring if she engaged in promiscuous copulations only with older neighbouring males who had at least survived past their first year.

#### Parental Investment & Mate Choice

The results of this study agree with Grant & Colgan's (1983) statement the "genetic quality of the male may be less important in that influencing mate choice than factors which directly affect the survival of the females' offspring." These factors are aspects of male quality directly affecting the female's fitness. They are important to the reproductive success of female American kestrels, which depends on the presence of a suitable nesting cavity and on the male's ability to provide food during most of the breeding season (Bent 1938; Willoughby & Cade 1964). Male raptors have a high parental investment before, during, and after fertilization (Newton 1979; Beissinger 1984). Males should vary considerably in their ability to provide and defend resources due to factors such as age or experience. Thus, the benefits to a discriminating female would be large under these circumstances. In general, as male parental investment increases, both the benefits and costs to choosy females increase (Fig. 2). To predict if females discriminate with respect to a given male cue, one would have to consider the species' natural history, local conditions (e.g. island versus mainland populations), male parental investment, etc. to estimate the relative costs and benefits illustrated in Figure 2. Given the

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acarcity of suitable nesting cavities (Hamerstrom <u>et al</u>. 1973), perhaps the search costs (Bengtsson 1978) for alternative male American kestrel genotypes outweigh the benefits. In this case, selection would not favour choosy females. The low frequency of natal philopatry (Bowman <u>et</u> <u>al</u>. 1985) and high mortality (Henny 1972) probably reduce inbreeding costs enough that behavioural incest avoidance mechanisms have not been favoured. Of the various mate choice strategies described by Wittenberger (1983), female kestrels most likely employ a thresholdcriterion based tactic. That is, females prefer only males able to provide sufficient resources for successful reproduction.

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Table I. Frequency of Occurrence of Observed Behaviours and Promiscuity in Captive American Kestrels.

		nest		food
year	n	inspection	copulation	transfer
1983	27a	26b(15)c	23 (6)d	14 (0)
1984	32	30 (22)	26 (11)	10 (1)
Total	59	56 (37)	49 (17)	24 (1)

a - 27 mate choice tests conducted.

b - nest inspections occurred in 26 tests.

c - female inspected both nest boxes in 15 tests.

d - female copulated with both males in 6 tests.

able II.Frequency Distribution of Female Mate Choice	with
Respect to Relatedness and Familiarity in Captive	
American Kestrels.	

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<b></b>	Sibling Exp	perience	محمد هند بلغة مشد بلغة علم علم علم الم
Choice*	Raised Together	Raised Apart	` Total**
Siblings	11	2	13
Non-Siblings	16	4	<b>, 2</b> 0

\*No significant difference in proportions (P=0.558, Fisher /Exact Probability Test). \*\*No significant difference between totals (P=0.149, One-tailed Normal Approximation to the Binomial).

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Table III. Frequency Distribution of Female Mate Choice with Respect to Relatedness and Relative Male Weight in Captive American Kestrels.

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(	Choice	****
Sibling	Non-Sibling	Total**
6	د 6	12
4	12/	16
	Sibling 6 4	Choice Sibling Non-Sibling 6 6 4 12/

\* Five tests omitted because males' average weights differed by less than 2 g. No significant difference in proportions (P=0.167, Fisher Exact Probability Test). \*\* No significant difference between totals (P=0.284, Onetailed Normal Approximation to the Binomial).

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# Fig. 1. Mate choice test pen for captive American kestrels.

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Fig. 2. The relative effects of increasing male parental investment (P.I.) on the costs and benefits to choosy females (based loosely on Parker 1983). Choosy females would be favoured to the right of A, whereas indiscriminating females would be favoured to the left.

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#### CONCLUSION

The techniques described herein enabled the determination of the influence of relatedness, weight and age on the mate choices of captive female American kestrels. Females apparently chose males at random with respect to the first two cues investigated, but chose two-year old experienced males significantly more often than one-year old inexperienced birds.

These results suggest that immediate gains, or resources, provided by the male, figure more prominently in the choice of mates by female kestrels than do specific traits reflecting male genetic quality. However, generalized indicators of male fitness, e.g. age, may be of importance.

The Macdonald Raptor Research Centre's colony provides an opportunity to continue investigations as to what other factors may influence mate choice in American kestrels (e.g. plumage, amount of food available to the displaying male, or male activity and vocalization). Hormone assays may determine whether individuals who make no choice are in breeding condition. For example, testosterone levels may affect the intensity of male courtship behaviour. The determination of any cues used by male kestrels to choose females and the relation of these cues to differences in the amount of energy invested by each sex in reproduction over the course of the breeding season should prove to be a fruitful avenue of future research.

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#### Key to Appendix A

1. Week & Pen Number : Gives the testing sequence.For actual dates see methods. Ľ 2. Male : S = Sibling N = Non-Sibling (F<0.02, see methods) II = Two-year old I = One-year old 3. Mate Choice Criteria : See methods for description. (Note that Location = % of time observed) 4. Choice : Categories below are decribed in methods.  $S = \bar{S}ibling$ N = Non-Sibling N.C. = No Choice Side = Chose Side 5. Previous Choice : The choice made by a female if tested previously in the same year. 6. Nesting Experience : T = Raised Together A = Raised Apart B and A refer to before and after the males' position was switched 7.

7. B and A refer to before and after the males' position was switched (see methods).

Appendix A. Summarized Nate Choice Data (1983)

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Mate Choice Criteria

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mb 9.		Loc	ation	Nest	Inspec.	Copu	latics	Food	Trans.	C1	101 C @	Pravious	Nachling
pen #	• male	8	A	B	A	B	A	B	Â	S/N	+/- wt.	Choice	Experience
1.1	S	4	0	1	, 0	0	0	0	Û				
	N	43	15	6	0	0	2 `	Û	0	N	+ 7g		T
1.2	S	37	48	0	1	0	4	0	0	\$	+12g		т
	N	14	13	0	0	0	0	0	0				
1.3	S	23	13	3	2	1	2	Ð	0	S	- 7g		T
	₩ -	16	0	2	0	0	Û	0	0		-		
1.4	S	27	24	1	2	0	l	0	0				
	N	62	43	3	1	7	4	2	0	N			T
1.5	S	21	14	0	0	0	0	0	0		• •		
	N	69	74	2	3	1	2	0	<b>+</b> 1	N	,		T
1.6	S	23	16	0	0	9	11	1	2	5	+ 3g		A
	N	58	34	7	2	0	3	0	0				
1.7	5	22	63	7	23	2	- 9	0	0	S			T
	H	12	7	10	Û	0	Û	Û	0				
1.8	S	2	34	0	3	1	2	0	0				
	H	69	4	6	0	0	Ú	1	Û	Side	I	i	A
1.9	S	3	5	0	Û	0	0	0	0				
	N	38	20	5	9	0	2	1	0	N	- 2g		A
		•									•		

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		Loc	ation	Nest I	nspec.	Copul	ations	Food	Trans.	Çħ	DICE	تیکند	Waablaaa
wk.& pen # 	sale	 B		B	A	B	A	 В 	A	5/N	+/- wt.	Previous Choice	Restling Experience
2.1	S	10	13	1	1	2	2	0	0				
	N (	12	46	0	1	4	3	2	1	N	- 2g	N	A
2.2	S	2	4	1	2	0	0	0	0				<b>,</b>
	H	70	43	10	4	4	5	2	i	N	<b>-</b> 5g		T
2.3	S	15	53	i	4	0	3	Ũ	0				
	H	53	0	2	0	5	Û	2	0	Side	,	5	T
2.4	S	58	3	1	1	0	Û	Û	0		•		
	N	8	61	2	2	0	0	0	0	N.C.		5	A
2.5	S	8	2	0	0	0	Û	0	0 .				
	N	23	9	_ 4	1	1	2	°,	0	N	- 9g	Ň	T
2.6	5	38	78	0	1	0	0	Ŷ	0				· ,
	N	50	17	0	0	0	0	Q	. 0	N.C.		N	T
2.7	S	3	8	0	0	0	0	0	0				
	N	4	27	2	2	4	4	0	1	N	+11g	S	A
2.8	S	12	Ð	0	0	0	0	0	0				-
	N	39	0	0	0	0	0	0	0	N.C.	4		T
2.9	S	14	9	4	2	2	2	0	1	S	+ 6g		T
	N	23	29	0	Û	0	0	0	Û				

### Mate Choice Criteria

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		Loc	ation	Nest	Inspec.	Сори	ation	s ` Food	Trans.	. Ch	01C2		<b>.</b>
wk.% pen #	male	 B	Â	B	A	B	A	, B	A ,	5/N	+/- wt.	Previous Choice	Nestling Experience
3.1	S N	6 8	5 3	2 1	2 1	0 0	0 0	0 0	0 0	N.C.			т
3.2	S N	62 13	82 0	1 0	0 0	- 0	1 0	, 0 0	1 0	s Vajs	- 4g		T
3.3	S N	9 79	33 9	0 5	0 2	, 0 , 7	0 3	0 0	0 0	N	- 4g	N	T
3.4	S N	60 29	0 50	2 0	Û Û	4 2	0 - 0	0 0	0 0	Side		X	. 1
3.5	s N	1 45	ھر 100 0	0	1 0	0	2 0	0 0	1 0	S	-30g	S,N.C.	<b>T</b>
3.6	S N	13 63	31 48	1 4	2 1	0 2	0 2	0- 1	0 1	N	- 5g	N	Т
3.7	S N	28 23	30 2	1 2	0 0	0 0	1 • 0	0 0	0 0	5			T
3.8	S N N	79 1	56 7	5 1	0 0	2 0	2 0	0 0	0 0	S	+ 4g		T
3.9	S - N "	31 30	8 32	10 10	8 4	4	6 5	0 2	0 0	N	+ 7g		T

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Appendix A. Summarized Mate Choice Data (1984)

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## Nate Choice Criteria

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		Loc	ation	Nest 1	nspec.	Сориі	ations	Food	Trans.	Ch	oice .	5	Neekla
nk.a pen <b>t</b>	male	B	A	B	A	B	A	 B	A	5/N	+/- wt.	' Choice	Restling Experience
								Ø					
1.1	S	29	11	9	2	10	5	ú	0				
	N	1	24	1	5	i	8	0	0	Side			A
1.2	S	34	5	4	2	0	0	i	0				
	N	6	7	0	0	0	Û	G	Ο.	N.C.			A
1.3	ΓS	8	20	5 الاستانية	2	0	0	ŷ	0				
	N	6	6	3	5	0	0	Û	0	N.C.		/ .	T
1.4	S	16	0	0	0	0	Û	t;	0		1•		
	N	73	60	7	2	0	1	Ģ	0	N	-30a		T
1.5	S	0	1	0	0	0	Ð	ţ	Û				
	N	8	0	0	Û	0	0	Ŷ	0	N.C.			T
1.6	Ś	0	1	0	0	0	0 <sup>.</sup>	e	0		•		
	М	77	90	4	9	7	7	C	0	N	- 69		T
1.7	S	59	30	3	2	4	5- ,	Ū	0	S.			A
	N	16	7	2	0	Û	0	ŷ	0		•		
1.8	5	63	16	2	2	7	3	e	0	S	+26g		T
	N	3	19	0	6	2	1	÷	0		-		

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## Mate Choice Criteria

		Loc	ation	Nest	Inspec.	Copul	ations	Food	Trans.		<sup>()</sup> Ch	oice	_	
wk.& pen #	male	 B	A	B	A	B	A	B	A		5/H	+/- wt.	Previous Choice	Nestling Experience
2.1	S	9	42	1	2	Ø	0	0	0					
	N	49	16	6	2	3	7	0	0		N	-15g		T
2.2	S	23	i	3	i	0	0	0	0					
	N	7	21	2	1	0	3	0	1		N	+ 3g		T
2.3	S	4	15 ·	0	0	0	0	0	0					
	N	1	0	0	0	0	Û	0	0	Ç	N.C.			T
2.4	5	4	0	4	0	0	0	Q	0					
	N	21	6	2	1	0	Q	0	Û		N.C.			T,
2.5	S	15	80	1	ູ 7	3	5	1	Û		S	+ 6g	н	Ţ
	N	56	0	1	0	1	0	1 Q	0					•
2.6 .	5	18	2	0	0	4	3	Ũ	U					
	N	38	53	2	2	4	8	Q	0		N	- 3g		A
2.7	S	31	15	5	2	8	4	Ō	ð		S	- 69		T
	N	5	5	0	0	0	Û	Û	0					٢
2.8	S	34	20	- 3	2	3	4	Û	0					
	N	5	24	5	5	4	5	1	1		N	+13g		T

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wk.& pen ‡	male	Location		Nest Inspec.		Copulations		Focd Trans,		Choice	`	
		<u></u> В,	A	B	A	`B	A	B	A	5/N +/- wt.	Previous Choice	Nestling Experience
7 1	c	L	40	٨	2	۵	7	٥	6			
3.1	N	52	14	7	0	1	Û	1	0	Side	S	T
<b>र</b> 7	ç	7	72	1		٥	0	ô	0			
5.1	N	44	18	4	0	6	4	, v V	0	N / -15g		T
3.3	5	10	45	i	2	2	3	Û	i			•
	N	43	28	7	0	4	0	2	0	51de		A
3.4	S	28	0	12	Û	0	0	Û	0 -			
	N	4	41	1	8	0	2	0	Û	Side		Ì T
3.5	5	21	0	1	Ú	4	Û	ŋ	0			
	H	56	83	2	3	2	8	1	2	N -29g	н`	T
3.6	5	11	8	2	2	3	3	0	0			
	N	36	21	9	6	8	4	Û	-0	N +13g		T
3.7	S	1	16	0	5	0	3	0	Û	•		`
	N	23	2	2	1	4	2	Ç	0	Side	S	T

## Mate Choice Criteria

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	male	<sup>°</sup> Mate Choice Criteria									
uk 1.		Location		Nest Inspec.		Copulations		Food Trans.		Choice	
wx.& pen #		 B ,	A	B	A	B	A	B	A	I1/I	+/- wt
3.8	П	89	77	11	10	8	5	0	0	11	, + 3g
	I	· 1	0	0	0	0	0	0	0		
4.1	II	11	19	<b>`</b> 4	4	4	5	0	0	п	- 7g
	I	0	22	1	0	0	0	0	0		•
4.2	11	66	32	5	8	5	10	0	0	11	+10g
د	I	9	23	0	1	0	Û	0	0		
4.3	11	41	74/	3	6	3	2	· 0	1	II	- 89
	I	43	0	1	0	0	0	0	0		-
4.4	11	74	50	1	0	6	0	0	0	11	+ 8g
р 1	١٠	0	25 .	0	0	0	0	. 0	0		
4.5	11	70	31	3	Û	1	0	2	0	П	+ 7g
	I	1	13	0	2	0	0	0	0		
4.6	11	44	4	, I	2	1	0	0	0		
	I	45	77	4	2	2	2	1	0	I	+20g
4.7	П	10	30	4	0	0	0	0	0		
	I	12	48	0	4	0	0	0 ′	0	N.C.	
4.8	н	73	14	3	1	4	0	1	i	11	+18g
•	I	10	31	0	0	0	0	0	0		
									·		

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