The adaptive significance of nest defence by merlin, *Falco columbarius*, males

CHRISTER G. WIKLUND

Department of Zoology, University of Gothenburg, P. O. Box 25059, S-400 31 Gothenburg, Sweden

Abstract. Observations during the laying period and after hatching showed that nest defence by merlins varied from fierce attacks to virtually no response. During the laying period as well as after hatching, the intensity of defence of paired males and females was inversely related. The frequency of nest desertions was higher among pairs in which the male invested little in nest defence compared with his mate than among other pairs. For females, intensity of nest defence was related to the age of the young and to the numbers of chicks. In contrast, these factors did not influence nest defence by males. The consequence of low investment in nest defence by males was a higher probability of the pair deserting the nest leading either to low fledgling production from replacement clutches or to complete breeding failure.

Offspring protection is one example of parental investment (Trivers 1972; Barash 1975), which has been elaborated in several models (Andersson et al. 1980; Patterson et al. 1980; Curio et al. 1984; Sargent & Gross 1985). Some studies have verified predictions of the models; i.e. defence of young increases with their age (Barash 1975; Weatherhead 1979; Andersson et al. 1980; Biermann & Robertson 1981; Curio & Regelmann 1982; Regelmann & Curio 1983), with brood size (Greig-Smith 1980; Carlisle 1985; Coleman et al. 1985) and with parental experience/age (Pugesek 1983; Shields 1984). Other studies, by contrast, have falsified the predicted relationships between intensity of nest defence and clutch/brood size and age of young (Knight & Temple 1986; Wallin 1987). Hence, there is a certain interspecific as well as intraspecific variation (e.g. Huntingford 1982; Weatherhead 1982; Knight & Temple 1986) in defence responses.

One explanation for intraspecific variation in nest defence is the adaptive modification of antipredator responses in relation to varying levels of predation (Tulley & Huntingford 1988), because certain predators pose a threat to the defending parent as well as to the young. In contests with predators, mobbing individuals sometimes become the victims of retaliatory attacks (Todd 1978; Buitron 1983; Walter 1983; Curio & Regelmann 1985). Thus, the intensity of brood defence is expected to affect the future lifespan of the parent (Wallin 1987). Survival might therefore be an important constraint on parental investment in nest defence.

The variability in intensity of nest defence is to a certain degree sex dependent in that males invest more in defence than do females (Wiklund & Stigh 1983; Shields 1984; Curio et al. 1985; Regelmann & Curio 1986; Burger 1987; Breitwisch 1988). The adaptive value of this behaviour is not well understood, however, because mobbing implies a deadly risk (Curio & Regelmann 1986). One advantage of mobbing of predators is that it may reduce the risk of nest predation (Knight & Temple 1988). It thus seems that females capitalize on the nest defence of their mates. On the other hand, a female initially invests more in the breeding attempt than the male. A high level of investment in nest defence by the male could reduce the initial inequality in reproductive effort between the sexes (Trivers 1972), and it would therefore be in the interest of the female to mate with such a male. Her choice among prospective mates seems to be facilitated by the males, because they advertise their boldness in defence by being more aggressive in the presence of their mates than when alone (Curio et al. 1985). Thus, selection of mates by females could be influenced by investment by males in nest defence. The red-winged blackbird, *Agelaius phoeniceus*, may provide such an example, as harem size is related to investment by males in nest defence (Knight & Temple 1988). But it is not clear whether vigorous defence affects a female's selection of a mate (Shields 1984; Breitwisch 1988) or is coupled with other qualities of the male (Holm 1973; Knight & Temple 1988; Tulley & Huntingford 1988).

There is evidence of raptors breeding less successfully because of nest predation (see Newton 1979), suggesting that nest defence may be beneficial. In the present study I focus on individual variability in nest defence among male and female

© 1990 The Association for the Study of Animal Behaviour

merlins. My aim was to examine (1) whether invest-
ment in nest defence increases with the age of the
young, (2) the variation in intensity of nest defence
among members of each pair, and (3) the adaptive
significance of male nest defence during the laying
period.

METHODS

I investigated nest defence by merlins in Padjelanta
National Park, northern Sweden. Padjelanta is a
high plateau with many lakes and rivers of varying
size, which are bordered with small birch *Betula sp.*
forests. Here, approximately 98% of the merlins
breed in old hooded crow, *Corvus corone cornix*,
nests while others breed on the ground or on cliff
ledges. In my study area, merlins have never been
persecuted by humans, because they are not a
threat to the economy of the reindeer, *Rangifer
tarandus*, herders living here.

   To investigate merlin nest defence behaviour, I
simulated a predation attempt by introducing a
stuffed raven, *Corvus corax*, near the merlins' nest.
Ravens are important nest predators, and they
elicit a stronger defence response from the merlins
than crows, for example. Moreover, ravens are
agile flyers with strong talons, which in a retaliatory
attack may hurt an attacking merlin. The stuffed
raven thus represented a potential threat to both
the nest contents and the defending bird. With
folded wings and in a vigilant position, the raven
was placed on top of a 2·5-m pole in an open area
about 5 m from the nest. This position enabled the
merlins to see the predator model clearly and
provided unimpeded access for attacking. Two
persons cooperated in each experimental trial.
When the male and the female were at the nest, the
raven was brought into position by a co-worker,
who then left the arena while the observer entered a
hide. Hence, the members of each pair received
similar treatment at the same time. After the exper-
iment was complete, the observer guarded the nest
area until the female returned to the nest or the nest
tree. This was done to ensure that the experimental
procedure did not allow crows to raid the merlins'
nest.

   I examined nest defence by males and females
among 29 randomly chosen merlin pairs during the
laying period. The breeding performance of all
pairs was repeatedly checked, once or twice a week,
until the chicks fledged. Of these pairs 26 reared

either the first or a replacement brood to hatching.
About a week after the eggs hatched, I again
recorded the nest defence behaviour using the same
procedure as in the experiments performed during
the laying period.

   Two experimental trials were run in 1984 and 27
during 1985–1986. Merlins breeding in this area
have been ringed with unique combinations of
colour rings each year since 1981. The ringing
scheme was enlarged during 1984, and since then
about 75% of all males and 95% of all females have
been equipped with colour rings. Since not all males
were ringed in 1985, I ran several experimental
trials in another study area during 1986. The dis-
tance between these areas is more than 50 km. In
successive years merlin males moved a mean ($\pm$ SD)
of $2·08 \pm 1·83$ km ($N = 19$). Therefore, I believe that
the risk of having run the experiment twice on the
same male is negligible.

   To check whether there was an association
between exposure time and intensity of nest
defence, I monitored the defence behaviour during
longer sessions among 23 merlin pairs. Each session
lasted from 4 to 45 min. Non-attacking was not
associated with the duration of the experiment. The
attacking birds attacked at a progressively lower
rate as the exposure proceeded. Attack frequencies
($\bar{X} \pm$ SD) during the first and second minute were
$5·78 \pm 6·28$ and $2·87 \pm 3·44$, respectively, among
males, and $1·30 \pm 2·92$ and $1·35 \pm 2·85$, respectively,
among females. I chose therefore to use the attack
frequency during the first minute after the raven
was discovered.

   For certain analyses, I classified individuals that
never attacked as non-attacking birds, and those
that attacked at least once as attacking birds,
although the range of defence responses seemed to
be continuous, as the distribution of attack fre-
quencies indicates (e.g. Fig. 1). Statistical methods
were used as described in Siegel (1956), Bradley
(1968) and Sokal & Rohlf (1981). Statistical tests
are two-tailed and means are given with 1 SD.

RESULTS

Individual Variability

   During the laying period, at least one member
of each of 25 merlin pairs attacked the stuffed
raven (Fig. 1). The probability of encountering an
attacking merlin was higher than 0·5 ($P < 0·001$,
binomial test), suggesting that the raven was recog-
nized as a potential predator. An attack was a
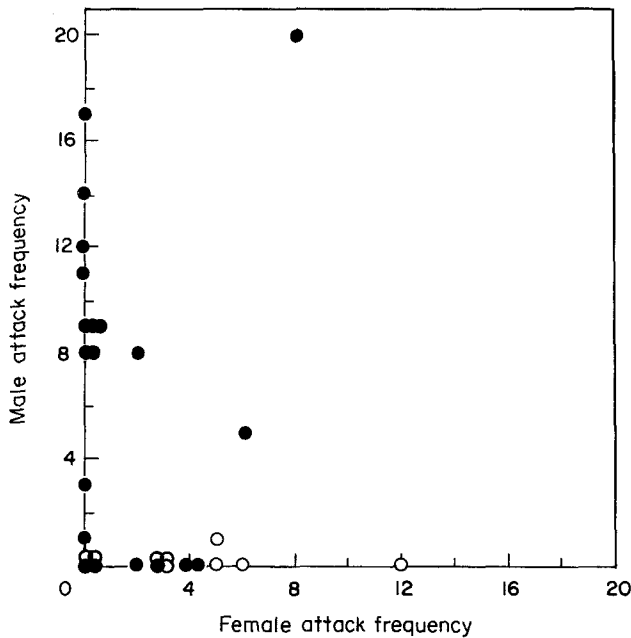
Figure 1. Frequencies of attack by the male and female of each pair of merlins during the laying period. ● Attack frequencies of birds that did not desert their nest; ○ attack frequencies of birds that deserted their nest.

swooping dive within less than 1 m of the raven, whose head and/or back was sometimes hit. The males' attacks were steep, almost vertical, dives in accelerating flight and with feet dropped. Females attacked more slowly and less steeply than males. Other merlins either left the nest area immediately or uttered alarm calls while circling about 5 m or more above the predator model, before they left. Shallow dips during flight at that height were not considered as attacks. The attack frequency ranged from one to 20 attacks among 15 males while 14 males did not attack the raven (Fig. 1). Similarly, female attack frequency varied greatly and ranged from one to 12 attacks among 14 females (Fig. 1). Fifteen females were classified as non-attacking birds.

About a week after the eggs hatched, records of nest defence behaviour were collected among those merlin pairs that had successfully reared either the first ($N=20$) or a replacement clutch ($N=6$) to hatching (three pairs failed completely before hatching). In the former category of merlin males, there were no significant differences in either the number of individuals attacking the raven or the attack frequency between the laying and the nestling periods ($P>0.50$, McNemar's test for the

significance of change, and $P>0.30$, Wilcoxon matched-pairs signed-ranks test), suggesting that male investment in nest defence could be independent of the age of the young. One of six males attending replacement broods attacked after the eggs hatched but not during the laying of the first clutch.

A predicted change in female nest defence was recorded after the eggs hatched, when more females with first broods had increased than had reduced the attack frequency (Fig. 2, $P>0.05$, one-tailed, McNemar's test for the significance of change). The attack frequencies between the two periods differed marginally, however (Fig. 2, $P<0.10$, one-tailed, Wilcoxon matched-pairs signed-ranks test). The increase in attack frequency (4.67 ± 2.71, $N=9$) probably varied too much among the birds for a significant effect to be obtained. In three females with replacement broods, the attack frequency decreased later in the season (Fig. 2).

Male and Female Defence Levels

During the laying period, there was no correlation between the defence levels of the members of each pair (Fig. 1, Spearman $r_s=-0.09$). But
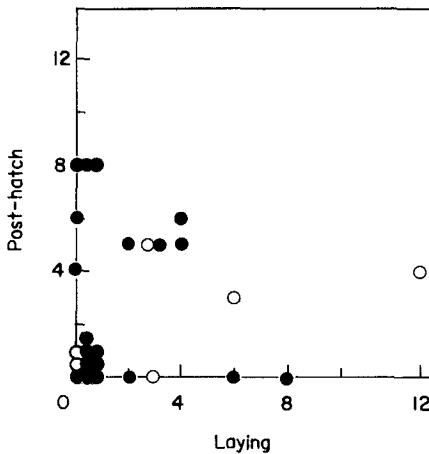
Figure 2. Frequency of attack by merlin females in relation to breeding stage. Each point represents the attack frequencies during the laying period and after hatching. Symbols as in Fig. 1.

the defence intensity was related to the sex of the bird, as the attack frequency was higher among attacking males than attacking females (males: $9·00 \pm 5·38$; females: $4·71 \pm 2·70$, $P < 0·05$, Mann–Whitney U-test). The attack frequency of females, but not of males, was negatively correlated with clutch size (Fig. 3a, $P < 0·05$, Pitman test). The proportion of attacks made by the male was positively correlated with clutch size (Fig. 3a, $P < 0·05$, Pitman test).

The defence levels of members of each pair were negatively correlated after the eggs hatched (Fig. 4, Spearman $r_s = -0·49$, $P < 0·05$). Moreover, the attack frequency of attacking males was not significantly different from that of attacking females (males: $8·54 \pm 5·05$; females: $6·11 \pm 1·45$, $P > 0·05$, Mann–Whitney U-test), presumably because female, but not male, attack frequency increased later in the season. This increase seemed to be related also to brood size, which was positively correlated with the number of attacks delivered by the female (Fig. 3b, $P < 0·05$, Pitman test). In contrast, the number of chicks was correlated with neither male attack frequency nor the proportion of attacks made by males.

Consequences of Nest Defence

Six of nine merlin pairs that deserted their first brood comprised an attacking female and a non-attacking male (Fig. 1). The proportions of attacks

made by males were $0·02 \pm 0·06$ among nest-deserting pairs and $0·65 \pm 0·46$ among other pairs. Thus, the male's contribution to the combined defence was lower among nest-deserting pairs than among other ones ($P < 0·01$, Mann–Whitney U-test). To examine the relationship between the male's contribution to the defence and nest desertion, I compared the frequency of nest desertion between two combinations of merlin pairs, i.e. attacking female/non-attacking male versus non-attacking female/attacking male. None of the 11 pairs in the latter category deserted whereas six out of 10 pairs in the former category deserted ($P < 0·05$, G-test). A similar result was obtained ($P < 0·01$, G-test), when all data were included in the analysis by using the attack frequencies to classify each pair into one of two categories, i.e. male versus female dominance in nest defence.

Three nest-deserting pairs failed completely while six others reared replacement broods. Such broods might produce fewer young than first ones (Newton 1986). Therefore, I compared reproductive performance among three categories of merlin pairs: pairs with attacking males ($N = 14$); pairs with non-attacking males that reared the first brood (faithful birds: $N = 6$); and pairs with non-attacking males that reared a replacement brood (re-nesting birds; $N = 6$).

Re-nesting birds had slightly smaller clutches than had birds of the other categories, but there were no significant differences in clutch sizes between the three categories of merlins (Fig. 5, $P > 0·20$, Kruskal–Wallis ANOVA). Re-nesting merlins were less successful after clutch completion. They experienced a lower hatching success than their conspecifics with a successful first breeding attempt (Table I, $P < 0·05$, Kruskal–Wallis ANOVA). Hence, re-nesting merlins did not rear as many nestlings as did other merlins (Fig. 5, $P < 0·01$, Kruskal–Wallis, ANOVA).

Attacking and faithful merlins, respectively, produced more fledglings than did re-nesting merlins (Fig. 5, $P < 0·05$, Kruskal–Wallis ANOVA). The low fledgling production by birds of the latter category was due to low hatching success and, to a certain extent, because they lost more chicks than did other merlin pairs (Table I). Among birds rearing first broods, the number of fledglings was positively correlated with female attack frequency ($P < 0·05$, Pitman test), as it was measured shortly after the eggs hatched. I have obtained a similar result using a larger sample (Wiklund, in press).
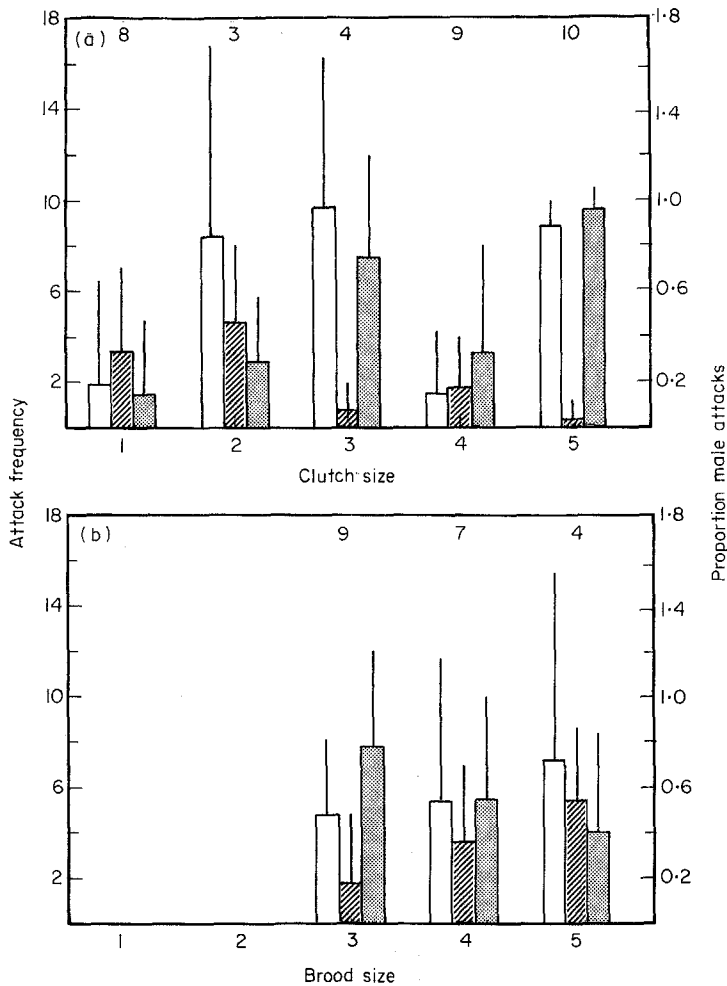
Figure 3. Frequency of attack by males and females and the male's contribution to the combined nest defence in relation to clutch and brood size (a) during the laying period and (b) about a week after hatching. Data are given as means + SD. Sample sizes are indicated in the figures. □; male attack frequency, ▨; female attack frequency, ▨; the proportion of attacks made by the male.

Fledgling production was correlated with neither male attack frequency nor the proportion of attacks made by the male.

DISCUSSION

Male and Female Defence Levels

For birds such as falcons, which do not build nests, access to nest sites is important (Village 1983). Although nests were available in excess each year in a large population of breeding hooded crows (Wiklund 1986), there were few nest sites far
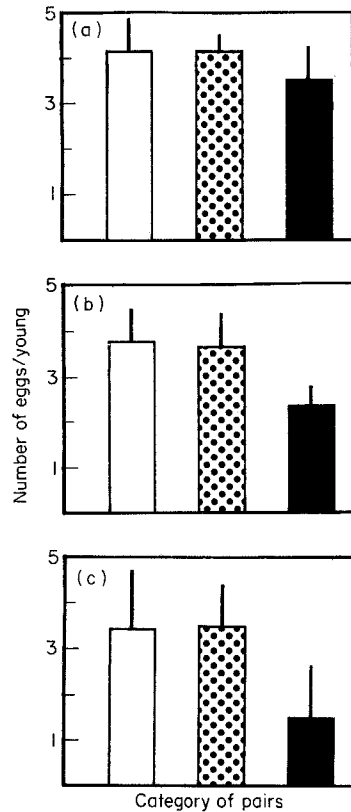
away from breeding crows. Some merlins thus bred as close as 10–20 m to a pair of nesting crows that regularly flew and foraged near the merlins' nest, unless they were attacked by the falcons, particularly the male. After a period of repeated mobbing, the crows avoided the defended area and used other flight routes and foraging areas. In early spring, merlin pairs seemed not to benefit from breeding close to a fieldfare, *Turdus pilaris*, colony, as they sometimes do later in the breeding season (Wiklund 1979) when the fieldfares are more aggressive against predators (Andersson et al. 1980) and defend a wide area around the colony including the
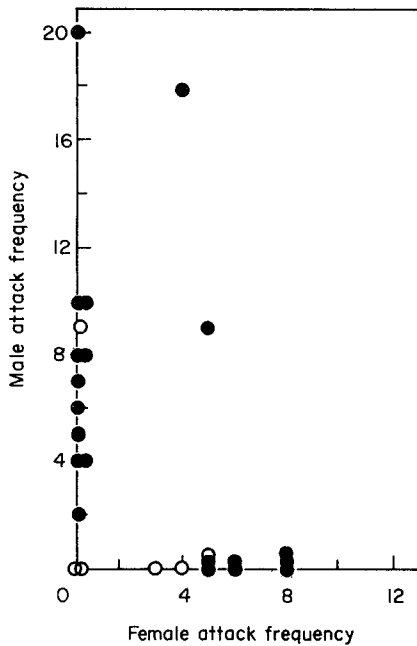
Figure 4. Frequency of attacks by the male and the female of each pair of merlins after hatching. ● Attack frequencies for birds that reared the first brood; ○ attack frequencies of birds that reared a replacement brood. Three merlin pairs failed to hatch any young.

Figure 5. Reproductive performance among three categories of merlin pairs. □: Pairs with attacking males ($N=14$); ⊞: pairs with non-attacking males that reared the first brood ($N=6$); ■: pairs with non-attacking males that reared a replacement brood ($N=6$). In the latter category of merlins, data are given for replacement broods. (a) Clutch size at completion. (b) Brood size about a week after hatching. (c) Fledgling production. Data are given as means + SD.

merlins' nest. Hence, the merlins seem to have few alternatives to nest defence especially in the early stages of the breeding cycle.

The predicted increase in nest defence with the age of the young has been verified among females of other birds (e.g. Barash 1975; Weatherhead 1979; Biermann & Robertson 1981; Knight & Temple 1986; Wallin 1987; this study). In some studies of males, by contrast, neither such a mechanism nor habituation have provided satisfactory explanations for the variance observed in male nest defence (Regelmann & Curio 1983, 1986; Curio et al. 1985; Curio 1987; Breitwisch 1988; Knight & Temple 1988). Similarly, the attack frequency of merlin males in the present study did not increase later in the season. Another factor affecting parental investment is brood size (Greig-Smith 1980; Carlisle 1985). In the merlins, it influences female nest defence (Wiklund, in press), suggesting that there is a combined effect of size and age of the brood on the intensity of female defence. In contrast, the male's contribution to nest defence increased with clutch size but not with the number of nestlings. Therefore, nest defence intensity and

the age and number of young, respectively, appear not to be as strongly associated in males as in females (see also Regelmann & Curio 1983), whose role in offspring protection seemed to change later in the season. These differences between the sexes suggest that, among males, the intensity of nest defence is an individually varying trait, which is independent of certain characteristics of the brood. Such an example of individual variability in aggressiveness may be difficult to obtain among birds of prey, because human persecution seems to have changed the proportions of aggressive and less aggressive individuals in several populations of raptors (Knight et al. 1989). The poor response to the value of the brood recorded for males could be

Table I. Hatching success and number of lost chicks ($\bar{X}\pm$ SD) among three categories of merlin pairs; pairs with attacking males and pairs with non-attacking males (faithful) both of which reared the first brood, and pairs with non-attacking males that reared a replacement brood (re-nesting)

Pairs with:	Attacking males	Non-attacking males	
		Faithful	Re-nesting
Hatching success	0·92±0·11 (14)	0·87±0·12 (6)	0·69±0·17 (6)
No. of lost chicks	0·35±0·81 (14)	0·17±0·37 (6)	0·83±0·89 (6)

A chick was classified as lost if it disappeared from the nest between two successive nest inspections, which were usually made each other day. Sample sizes are within parentheses.

related to sex role partitioning of parental duties. The role of the female would give her better opportunities, particularly after the eggs hatch, to assess the value of the brood. At that time, the hunting male rarely visits the nest but delivers food, at some distance from the nest, to the female who then feeds the young. Before the eggs hatch, however, the male sometimes sits on them (Newton 1979). Thus, it is likely that other factors that provide distinct and easily accessible information on the consequences for the fitness of the male influence his investment more than do the age of the young and brood size. My observations suggest that the risk of nest desertion by the female is such a factor.

Theoretical arguments suggest that adult size, weight and age influence parental care of young (Andersson & Norberg 1981; Carlisle 1982; Curio et al. 1984). In the present study, however, attacking and non-attacking males did not differ significantly in wing chord ($201·0\pm3·9$ mm, $N=17$, and $200·7\pm0·9$ mm, $N=4$, respectively), tarsus length ($36·0\pm0·9$ mm, $N=16$, and $35·8\pm1·1$ mm, $N=4$, respectively) and body mass ($167·8\pm7·8$ g, $N=17$, and $172·3\pm5·5$ g, $N=4$, respectively). In addition, there were no significant differences in size and body mass, respectively, between the mates of the two categories of males (the mates of attacking males first, wing chord: $218·5\pm4·4$ mm, $N=13$, and $220·2\pm4·2$ mm, $N=9$, respectively, tarsus length: $37·7\pm1·1$ mm, $N=13$, and $37·8\pm1·1$ mm, $N=6$, respectively, body mass: $228·1\pm12·0$ g, $N=13$, and $229·1\pm19·7$ g, $N=8$, respectively). There is no evidence that parental age affects nest defence (Breitwisch 1988). Similarly, exposures of the raven to individually known merlins during successive breeding seasons have not demonstrated

consistently different responses from those of previous seasons (unpublished data).

Consequences of Nest Defence

Nest predation is one cause of breeding failure among merlins. In my study area, about one-third of the breeding attempts fail due to predation (1979, unpublished data) while in other areas nest predation may account for 50% or more of the failures (I. Newton, personal communication). Five nests contained eggshell remains indicating that predation might have caused nest desertion. This was also caused by frequent movements of predators near the merlins' nest. Thus, one female abandoned her nest, and moved about 200 m to another one, after several contests with crows.

Most pairs comprised one attacking and one non-attacking bird: i.e. either the male or the female attacked. It is not yet clear whether this sex role partitioning of nest defence is consistent during an individual's life or varies from one season to another depending on the mate of each breeding season. The investment in nest defence by the male was important, in that nest desertion was frequent among pairs in which the male contributed less than his mate to the defence. During the laying period, raptor females are unusually heavy (Newton 1979), and, therefore, less agile in flight (Andersson & Norberg 1981). They are then exposed to higher risks in contests than at other times of the year. A male investing little in nest defence may therefore impose certain risks on his mate, if this forces her to make a large effort in nest defence. Deserting the nest, or attacking predators at a low frequency, which sometimes

results in nest predation, seemed to be alternatives for females mated with non-attacking males. Conceivably, the low attack frequency by females might have depended on the need to reduce the risk of injury, as retaliatory assaults by predators could be fatal (Broun 1947; Todd 1978; Buitron 1983; Walter 1983). In areas with many predators, such strategies should confer less risk to the female than those entailed during intense nest defence, although, by doing this, she might sacrifice the brood. If nest desertion occurs early, however, the risk of a total failure is reduced as there is still time to rear a replacement brood (Newton 1986).

There is evidence from stonechats, *Saxicola torquata*, and eastern kingbirds, *Tyrannus tyrannus*, that nest defence and breeding success are associated (Greig-Smith 1980; Blancher & Robertson 1982), and in red-winged blackbirds nest survival is correlated with intensity of nest defence (Knight & Temple 1988). The costs associated with low investment in nest defence by merlin males in the present study were complete breeding failure and low fledgling production from replacement broods. Clutch size did not limit reproductive success for re-nesting birds. The low fledgling production was due to reduced hatching success and somewhat heavier chick losses among replacement broods than among first ones. It is conceivable that these merlins repeatedly invested less in parental care than did the other ones. For instance, predators raided one-third of the replacement broods. The birds that deserted their nests and were not located again probably did not breed. They were late breeders, and such birds rarely produce a replacement clutch (Newton 1986).

Another cost experienced by most females mated with non-attacking males was a high investment in nest defence. This seems to reduce the future reproductive lifespan of the female (Wallin 1987) and may thus affect her lifetime reproductive success. It depends in part on the number of successful breeding attempts (Newton 1985). I used data from one breeding attempt of each bird. This is a poor estimate of fitness particularly among longlived birds such as merlins. Thus, my data may not accurately estimate the relationship between nest defence and fitness. There is, however, a certain degree of repeatability of brood size among merlin females (unpublished data), which, for a comparison of categories, could allow approximating fitness from only one breeding attempt.

Given this, male investment in nest defence is expected to influence mate selection by females (Maynard Smith 1977), although such evidence has not been obtained (Breitwisch 1988). This could be because mate selection by the female is not a simple choice based on the male's nest defence ability. Selander (1965) suggested that a nest area with few predators could comprise a secondary sexual character among males, and might determine female choice. This may apply to red-winged blackbirds as male territories providing safe nests attract most females (Holm 1973): the males obtain such territories either by selecting a territory with a certain type of vegetation or by defending the territory against predators (Holm 1973; Knight & Temple 1988). Similarly, in areas with few predators the breeding success of non-attacking merlin males may be similar to that of attacking ones in other areas. This explanation is supported by the fact that the overall fledgling production of attacking and non-attacking merlin males did not differ significantly. Before this explanation is fully accepted, however, further studies discriminating between female choice of mates and of nest sites are needed.

REFERENCES

Andersson, M. & Norberg, R. A. 1981. Evolution of reversed sexual size dimorphism and sex role partitioning among birds of prey with a size scaling of flight performance. *Biol. J. Linn. Soc.*, **15**, 105–130.

Andersson, M., Wiklund, C. G. & Rundgren, H. 1980. Parental defence of offspring: a model and an example. *Anim. Behav.*, **28**, 536–542.

Barash, D. P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. *Wilson Bull.*, **87**, 367–373.

Biermann, G. C. & Robertson, R. J. 1981. An increase in parental investment during the breeding season. *Anim. Behav.*, **29**, 487–489.

Blancher, P. J. & Robertson, R. J. 1982. Kingbird aggression: does it deter predation? *Anim. Behav.*, **30**, 929–930.

Bradley, J. V. 1968. *Distribution-free Statistical Tests.* Englewood Cliffs, New Jersey: Prentice–Hall.

Breitwisch, R. 1988. Sex differences in defence of eggs and nestlings by northern mockingbirds, *Mimus polyglottos. Anim. Behav.*, **36**, 62–72.

Broun, D. P. 1947. Golden eagle captures red-shouldered hawk. *Auk*, **6**, 317–318.

Buitron, D. 1983. Variability in the responses of black-billed magpies to natural predators. *Behaviour*, **87**, 209–236.

Burger, J. 1987. Selection for equitability in some aspects of reproductive investment in herring gulls *Larus argentatus. Ornis Scand.*, **18**, 17–23.

Carlisle, T. R. 1982. Brood success in variable environments: implications for parental care allocation. *Anim. Behav.*, **30**, 824–836.

Carlisle, T. R. 1985. Parental response to brood size in a cichlid fish. *Anim. Behav.*, **33**, 234–238.

Coleman, R. M., Gross, M. R. & Sargent, R. C. 1985. Parental investment decision rules: a test in bluegill sunfish. *Behav. Ecol. Sociobiol.*, **18**, 59–66.

Curio, E. 1987. Brood defence in the great tit: the influence of age, number and quality of young. *Ardea*, **75**, 35–42.

Curio, E. & Regelmann, K. 1982. Fortpflanzungswert und 'Brutwert' der Kohlmeise (*Parus major*). *J. Ornithol.*, **123**, 237–257.

Curio, E. & Regelmann, K. 1985. The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Z. Tierpsychol.*, **69**, 3–18.

Curio, E. & Regelmann, K. 1986. Predator harassment implies a deadly risk: a reply to Hennessy. *Ethology*, **72**, 75–78.

Curio, E., Regelmann, K. & Zimmermann, U. 1984. The defence of first and second broods by the great tit (*Parus major*) parents: a test of predictive sociobiology. *Z. Tierpsychol.*, **66**, 101–127.

Curio, E., Regelmann, K. & Zimmermann, U. 1985. Brood defence in the great tit (*Parus major*): the influence of life-history and habitat. *Behav. Ecol. Sociobiol.*, **16**, 273–283.

Greig-Smith, P. W. 1980. Parental investment in nest defence by stonechats (*Saxicola torquata*). *Anim. Behav.*, **28**, 604–619.

Holm, C. H. 1973. Breeding sex ratios, territoriality and reproductive success in the red-winged blackbird (*Agelaius phoeniceus*). *Ecology*, **54**, 356–365.

Huntingford, F. A. 1982. Do inter- and intraspecific aggression vary in relation to predation pressure in sticklebacks? *Anim. Behav.*, **30**, 909–916.

Knight, R. L. & Temple, S. A. 1986. Why does intensity of avian nest defence increase during the nesting cycle? *Auk*, **103**, 318–327.

Knight, R. L. & Temple, S. A. 1988. Nest-defense behavior in the red-winged blackbird. *Condor*, **90**, 193–200.

Knight, R. L., Andersen, D. E., Bechard, M. J. & Marr N. V. 1989. Geographic variation in nest-defence behaviour of the red-tailed hawk (*Buteo jamaicensis*). *Ibis*, **131**, 22–26.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.*, **25**, 1–9.

Newton, I. 1979. *Population Ecology of Raptors.* Berkhamstead: T. & A. D. Poyser.

Newton, I. 1985. Lifetime reproductive output of female sparrowhawks. *J. Anim. Ecol.*, **54**, 241–253.

Newton, I. 1986. *The Sparrowhawk.* Calton: T & A. D. Poyser.

Patterson, T. L., Petrinovich, L. & James, D. K. 1980. Reproductive value and appropriateness of response to predators by white-crowned sparrows. *Behav. Ecol. Sociobiol.*, **7**, 227–231.

Pugesek, B. H. 1983. The relationship between parental age and reproductive effort in the California gull (*Larus californicus*). *Behav. Ecol. Sociobiol.*, **13**, 161–171.

Regelmann, K. & Curio, E. 1983. Determinants of brood defence in the great tit *Parus major* L. *Behav. Ecol. Sociobiol.*, **13**, 131–145.

Regelmann, K. & Curio, E. 1986. Why do great tit (*Parus major*) males defend their brood more than females do? *Anim. Behav.*, **34**, 1206–1214.

Sargent, C. R. & Gross, M. R. 1985. Parental investment decision rules and the Concorde fallacy. *Behav. Ecol. Sociobiol.*, **17**, 43–45.

Selander, R. K. 1965. On mating systems and sexual selection. *Am. Nat.*, **99**, 129–141.

Shields, W. M. 1984. Barn swallow mobbing: self-defence, collateral kin defence, group defence, or parental care? *Anim. Behav.*, **32**, 132–148.

Siegel, S. 1956. *Non-parametric Statistics for the Behavioural Sciences.* Tokyo: McGraw–Hill.

Sokal, R. R. & Rohlf, F. J. 1981. *Biometry.* New York: W. H. Freeman.

Todd, D. M. 1978. Golden eagle killing buzzard. *Br. Birds*, **73**, 536–537.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. London: Heinemann.

Tulley, J. J. & Huntingford, F. A. 1988. Additional information on the relationship between intra-specific aggression and anti-predator behaviour in the three-spined stickleback, *Gasterosteus aculeatus. Ethology*, **78**, 219–222.

Village, A. 1983. The role of nest-site availability and territorial behaviour in limiting the breeding density of kestrels. *J. Anim. Ecol.*, **52**, 636–645.

Wallin, K. 1987. Parental defence as parental care in tawny owls (*Strix aluco*). *Behaviour*, **102**, 213–230.

Walter, D. 1983. Golden eagle killing mobbing carrion crow. *Br. Birds*, **76**, 312.

Weatherhead, P. J. 1979. Do savannah sparrows commit the Concorde fallacy? *Behav. Ecol. Sociobiol.*, **5**, 373–381.

Weatherhead, P. J. 1982. Risk-taking by red-winged blackbirds and the Concorde fallacy. *Z. Tierpsychol.*, **60,** 199–208.

Wiklund, C. G. 1979. Increased breeding success for merlins *Falco columbarius* nesting among colonies of fieldfares *Turdus pilaris. Ibis*, **121,** 109–111.

Wiklund, C. G. 1986. *The Bird Fauna of Padjelanta National Park.* Stockholm: Swedish National Board of Environmental Protection.

Wiklund, C. G. In press. Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defence of young. *Behav. Ecol. Sociobiol.*

Wiklund, C. G. & Stigh, J. 1983. Nest defence and evolution of reversed sexual size dimorphism in snowy owls *Nyctea scandiaca. Ornis Scand.*, **14,** 58–62.