

Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young

Christer G. Wiklund

Department of Zoology, University of Gothenburg, P.O. Box 250 59, S-40031 Gothenburg, Sweden

Received November 29, 1988 / Accepted October 19, 1989

Summary. Nest predation was simulated by presenting a stuffed raven close to nests of merlins. This was done to examine the influence of brood size related factors on female defence intensity. The original clutch size did not affect nest defense after hatching, but brood size was important. It determined the attack frequency and, for each brood size level, the proportion of attacking females. When brood sizes were manipulated, the defense intensity increased and decreased, respectively, in relation to the size of the brood. In addition, broods with high future survival (first broods) were defended more vigorously than broods with low future survival (replacement broods). Hence, expected benefits in terms of fledgling production and chick survival seem to be important determinants of female investment in offspring protection. The lower predation rate among females responding with overt aggression to the raven compared to that of less aggressive females suggests that defence of young is beneficial.

Introduction

Parental investment theory suggests that expected benefits rather than past investment should determine the level of investment in parental care (Dawkins and Carlisle 1976; Maynard Smith 1977). Theoretical arguments for such a mechanism regulating parental investment by animals is widely accepted, although conclusive evidence is lacking (Robertson and Biermann 1979; Dawkins and Brockmann 1980; Weatherhead 1982; Carlisle 1985; Colemann et al. 1985). One reason seems to be that expected benefits and past investment are not always independent. It is therefore important to uncouple these variables.

Defense of offspring is one example of parental investment that improves survival of young (Greig-Smith 1980; Blancher and Robertson 1982). The positive correlations between nest defense and brood size and production of young have been taken as evidence that expected benefits determine parental care (e.g., East 1981; Wallin 1987). But there may be hidden variables influencing such correlations. For instance, brood size and the number of young surviving to breeding age depend on the time at which breeding starts (Newton and Marquiss 1984; Meijer 1988). This is, in turn, related to foraging success, and, among raptors and owls, to mainly male foraging success (Taylor 1975; Newton 1979). Another confounding variable is body size, which has been proposed to be associated with nest defense (e.g., Andersson and Norberg 1981). Therefore, experiments simultaneously controlling other variables may provide stronger evidence compared to correlations.

In the merlin *Falco columbarius*, males and females may defend the nest against predators, and, within a pair, it is common that one of the mates invests more in nest defense than the other does (Wiklund, in press). The defense intensity of males is neither related to age of young nor to brood size, but is an individually varying trait (Wiklund, in press). The rules for parental investment may thus differ between males and females. This study examined offspring protection by merlin females with emphasis on expected benefits as a possible mechanism for determining the nest defense intensity. I predicted that (a) defense intensity should be related to the expected benefit, as determined by brood size, and not to past investment, as measured by original clutch size, b) defense intensity should increase and decrease, respectively, when brood sizes are experimentally increased and decreased, c) replacement broods should receive less

care than first broods – because of low survival among late compared to early fledglings (Newton and Marquiss 1984) and the parent's reduced ability to care for young due to the extra loss of energy associated with producing a replacement brood, and d) nest defense intensity and the risk of predation are inversely related.

Study area and general methods

This study was pursued in Padjelanta National Park, N Sweden, from 1984 to 1988. It is an alpine area in the transition zone between tundra and forest, with several lakes and rivers bordered by birch *Betula sp.* forests of varying size. Here, merlins nest among old hooded crow *Corvus cornix* nests. The nests were about 5 m or more above the ground and therefore safe from ground predators such as the common red fox *Vulpes vulpes* and the wolverine *Gulo gulo*. In this study area, common avian nest predators such as hooded crows and ravens *Corvus corax* sometimes raid one-third of the merlin nests in a given breeding season (Wiklund 1979; Wiklund, unpublished data). To distinguish between nest predation and nestling mortality due to starvation among broods less than 10 days old, I classified the complete loss of a chick as a case of predation because, in the case of starvation, the chick or parts of it remained in the nest during a longer time than the duration between two successive nest visits (every other day). Nests with chicks older than 10 days were visited 1–2 times a week until fledging. However, in this 12-year study of merlins, there was no record of chick losses due to starvation among nestlings older than 10 days.

I examined female investment in nest defense by simulating a predation attempt. In all experiments, a stuffed raven was introduced near the nest of a merlin pair. Ravens sometimes respond with retaliatory attacks on mobbing merlins. Therefore, the stuffed raven predator model combined a threat to the chicks as well as to the adult merlin. The raven, with folded wings and in a vigilant position, was mounted on top of a 2.5 m pole in order to resemble a live bird searching for food. The predator model was placed in an open area about 5 m from the merlins' nest. This position ensured that the merlins would see the model and have unimpeded access for attacking. The raven was brought into position by a co-worker, who immediately left the area. I was positioned in a well-camouflaged hide in order to record female nest defence behaviour. Thus, each merlin was left undisturbed by us during exposure to the predator model. When the female discovered the raven, her flight suddenly changed (i.e., a dip or climb in the flight, an attack on the raven or a sharp turn away from it), and she gave alarm calls in flight over the raven. The responses that followed upon discovery varied from fierce attacks on the raven to leaving the nest area. The attacks were performed as swooping dives within 0.5 m of the back and the head of the raven, which sometimes were hit by the female's talons and/or body. Shallow dips in flight well above the raven were not considered as attacks. Each attacking bird repeatedly attacked the model, whereas non-attacking birds never approached closer than 4–5 m of the raven. The time of exposure did not change nest defence behaviour. However, there was a relationship between time and nest defense intensity, i.e., the attack frequency declined as the exposure time increased (Wiklund, in press). Therefore, the attack frequency during the 1 min after discovery was used as a measure of female defense intensity.

Experiment I investigated offspring protection by females rearing broods of varying size. Each female was tested once

about 1 week after hatching. Later in the season, the falcons were color-ringed to avoid repeats of experiments on the same bird. All the birds tested in 1984 ($n=8$) were color-ringed. Although most females were ringed in 1985 and 1986, some of these birds were not captured. Therefore, the trials during 1986 ($n=11$) and 1987 ($n=7$) were run in different study areas about 50 km away from the ones used during previous years. Movements of females between successive breeding seasons were 1379.2 ± 365.4 m ($n=12$). Thus, I consider that the risk of double experimental trials on the same bird was negligible. In some of the calculations, the attack frequencies of five females were excluded because unusually poor weather conditions during the trials affected the birds' attack rate.

Experiment II compared offspring protection by females when they reared large and small broods. In 1986, 12 merlin pairs were randomly selected in early spring for this study. Before the experimental trials started about 1 week after hatching, nest predation had reduced the number of experimental birds to 11 pairs. I used a blocking procedure combining 2 females with chicks of equal age in each block for a total of 5 complete blocks. For each block, coin tossing determined which one of the broods to reduce to two young and which one to enlarge to five or more young. Chicks were then transferred within each blocks. The 11th female received young from two other broods. This made it possible to obtain data from all females. The body size of transferred chicks was intermediate to that of the chicks in the host nest, i.e., the transferred chicks became neither the largest nor the smallest ones. Manipulated broods were left for about a day (28.8 ± 2.3 h) before examination of female offspring protection. After these trials, chicks were again transferred within each block, the brood sizes in each pair of nests being reversed, and the trials repeated about 1 day later (28.6 ± 2.1 h). Each female was tested once for each brood size level according to the procedure used in Experiment I.

Experiment III examined defence of first and replacement broods among individually known females. From 1985 to 1988, data were collected among seven females that produced a replacement brood after failure earlier in the season. I then used data on attack frequencies during laying of the first brood and after hatching of the replacement brood. Thus, the time span between the trials was approximately 6 weeks. Moreover, the data include also observations from two females that successfully reared their first broods and, another year, produced and tended a replacement brood after loss of the first one.

To examine the association between nest defense and size and body mass, respectively, I compared wingchord (method 3 in Svensson 1975), tarsus length, and weight between attacking and non-attacking females. The body mass was determined with an accuracy of 1 g. Wingchord and tarsus length of the right leg, from one joint to the other, were measured to the nearest 1 mm and 0.1 mm, respectively.

Unless otherwise stated, two-tailed statistical tests have been used as described in Sokal and Rohlf (1981) and Siegel (1956). Means are given with 1 SE.

Results

Experiment I: Clutch versus brood size as determinant of nest defense by females tending natural broods

Fifteen females attacked the raven while 25 others did not. Several females of the latter category left the nest area when they were exposed to the raven.



Fig. 1. The reproductive performance of merlin females in relation to their nest defense behavior during simulation of nest predation. Unshaded bars (□) denote attacking females; shaded bars (■) non-attacking females. Clutch size, brood size and fledgling number are given as means with 1 SE. Sample sizes are given in the text

The defense intensity of attacking females was 6.40 ± 0.61 attacks.

Except for 5 non-attacking females that had 3 eggs each, clutch sizes were 4 or 5 eggs. There was no significant difference in original clutch size between attacking (4.40 ± 0.14) and non-attacking (4.05 ± 0.15) birds (Fig. 1, $P = 0.10$, Mann Whitney U-test).

When I ran the trials, brood sizes ranged from three to five young among attacking females, and between one and five young among non-attacking females. There was an association between nest defense intensity and brood size. The proportion of attacking individuals was thus higher among females with large broods than among females with small ones (Fig. 2, $P < 0.05$, G-test). To distinguish between the effects of clutch and brood size, respectively, on female defense intensity, I ran a partial correlation analysis. It indicated that the attack frequency was positively correlated with brood size ($r = 0.334$, $t = 1.94$, $P < 0.05$, one-tailed) but not with original clutch size ($r = -0.048$).

Experiment II: The effect of brood size manipulations on nest defense intensity

In the first set of trials, all females with enlarged broods attacked the predator, whereas none with reduced broods did so. The results of the second set, in which females with enlarged broods now had reduced ones and vice versa, were less clear-cut: 2 females with enlarged broods attacked and 4 did not, and 3 females with reduced broods did not attack and 2 did. Nevertheless, the mean attack

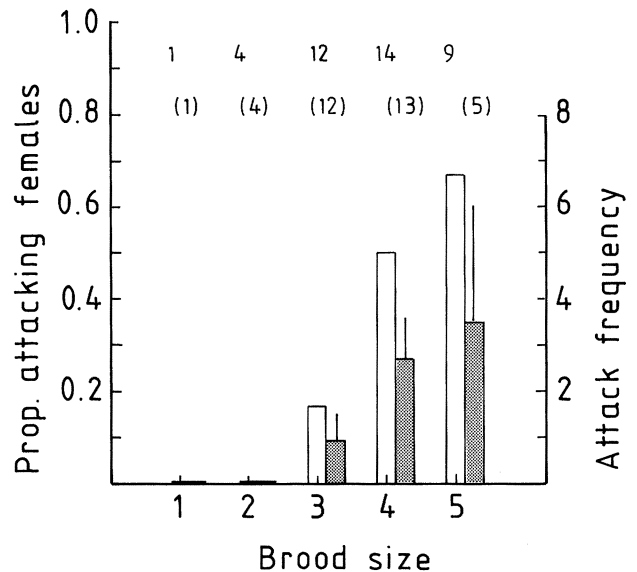


Fig. 2. The relationship between female nest defense intensity at hatch and brood size. Unshaded bars (□) show for each brood size level the proportion of females that attacked. Sample sizes are indicated. Shaded bars (■) show the attack frequency of females tending broods of varying size. The attack frequency was measured during the 1 min following discovery of the raven. Means ± 1 SE are given. Data from five attacking females were omitted because poor weather conditions affected their attack rates. Sample sizes are indicated within parentheses

frequency of the females was greater when they defended enlarged broods than when they defended reduced ones (3.55 ± 1.06 and 0.73 ± 0.53 , respectively). A non-parametric, pairwise permutation test [Bradley 1968; H_0 (null hypothesis): similar investment in offspring protection by each female and independent of brood size] showed that females defended enlarged broods more vigorously than they defended reduced ones ($P < 0.02$).

Experiment III: Defense of first versus replacement broods

Five of 9 females responded with attacks on the raven when they tended first broods. With one exception, all females seemed to invest less in defense of replacement broods than first ones. For instance, 2 females with four young each in the first and the replacement brood reduced their attack frequencies by 100% and 75%, respectively. The attack frequency was thus higher when first broods were defended (Table 1, $P < 0.05$, Wilcoxon matched pairs test), although the two categories of broods did not differ in size ($P > 0.20$, Mann-Whitney U-test).

Table 1. The attack frequencies of merlin females when they tended young of varying survival value. The young of first broods were considered to have higher probability of survival compared to young in replacement broods. Attack frequencies and brood sizes are given as means \pm 1 SE

	First broods	Replacement broods
Attack frequency	4.3 \pm 1.5	1.1 \pm 0.5
Brood size	2.0 \pm 0.7	2.1 \pm 0.4

Table 2. Weight, body size, and condition index of attacking and non-attacking merlin females. Data are given as means \pm 1 SE. Sample sizes are shown within parentheses

	Attacking females	Non-attacking females
Weight (g)	223.0 \pm 4.6 (10)	227.4 \pm 3.6 (16)
Wingchord (mm)	219.9 \pm 1.7 (14)	220.2 \pm 1.1 (17)
Tarsus-length (mm)	38.0 \pm 0.3 (12)	37.5 \pm 0.2 (17)
Condition index*	0.160 \pm 0.002 (10)	0.163 \pm 0.001 (16)

* The condition index is $\frac{\sqrt[3]{\text{weight}}}{\text{tarsuslength}}$

Nest defence in relation to size, body mass and condition

There did not seem to be any size differences between non-attacking and attacking birds, as neither wingchord nor tarsus length differed significantly between the two categories of females ($P > 0.60$ and $P > 0.10$, Mann Whitney U-test), although the latter ones had slightly longer tarsi (Table 2).

To examine the relationship between parental care and nutrition status, I compared body mass and condition between the two categories of females. I then used the cube root of weight divided by tarsus length as a measure of condition. Such a condition index controls to a certain extent the size variation among the birds. There were no significant differences in body mass and condition index between attacking and non-attacking females (Table 2; in both cases, $P > 0.30$, Mann Whitney U-test). The small sample size, however, calls for a cautious interpretation of these results.

The adaptive significance of female nest defence

When I ran the trials about 1 week after hatching, the brood sizes differed significantly between attacking, 4.27 \pm 0.19, and non-attacking females,

3.28 \pm 0.21 (Fig. 1, $P < 0.01$, Mann-Whitney U-test).

Each of 13 attacking females produced four or five fledglings while another 2 females produced three and two young, respectively. The fledgling production by non-attacking females was more varied, ranging from five fledglings to nil, and only 8 of those females produced more than three fledglings. The attacking females raised thus more fledglings, 4.20 \pm 0.23, than did the non-attacking ones, 2.84 \pm 0.21 (Fig. 1, $P < 0.01$, Mann-Whitney U-test).

The difference in brood size between the two categories of females was slightly higher at fledging (about 1.4 young) compared to shortly after hatching (about 1.0 young). This was caused by chick losses occurring in the period between the trials and fledging. One chick belonging to an attacking female was weak, but alive, when I ran the trial. Two days later, however, this chick, which was still in the nest, was dead, probably because of starvation or sickness. Two non-attacking females lost their entire broods of two and of three young, respectively, due to nest predation. The latter brood fell victim to an attack by a rough-legged buzzard *Buteo lagopus*, which collected all the merlin chicks within a couple of hours. In addition, 6 other non-attacking females lost one chick each. No chick or part of it was left in the nests of these females. Therefore, I consider predation to be the cause also behind these losses. Thus, the non-attacking females experienced more chick losses due to nest predation than did the attacking ones ($P < 0.05$, G-test).

Discussion

Brood size and offspring protection

In birds of prey, the female invests much in egg production, e.g., the mass of a merlin's clutch of five eggs is similar to 50–60% of the adult female's body mass (Newton 1979). Moreover, some of the female's energy reserves are used during incubation. During this period, the amount of energy required by the female is related to clutch size and ambient temperature because, below a critical temperature, the energetic expenditure increases with clutch size (Biebach 1981; Haftorn and Reinertsen 1985). It is likely that the thermoneutral zone for incubating merlin females is higher than the average ambient temperature of my study area, which varies between 3° C and 12° C during the incubation period. I presume, therefore, that up until

hatch, clutch size may be a reasonable measure of past investment.

In some species, there is a positive correlation between nest defense during the incubation period and clutch size (Robertson and Biermann 1979; Windt and Curio 1986). After hatching, by contrast, the level of female offspring protection may not be correlated with clutch size (Wallin 1987). This study showed that the proportion of females attacking the predator as well as the attack frequency depended on brood size but not on past investment, i.e., original clutch size. Hence, the effect of clutch size on female defense intensity seems to vary with the stage of the breeding cycle. It is conceivable that with some egg/hatching loss the nestling number may not match previous clutch size. The brood size at hatch would therefore be a better predictor of success, and consequently a positive correlation between defense intensity and brood size is expected. Such a correlation requires careful interpretation, however, since there may be hidden variables correlated with defence intensity as well as brood size.

A better test of the effect of brood size on defense intensity would be to examine the parent's ability to adapt the defence level to varying brood sizes. Such evidence has been obtained in studies of animals with monoparental care (Carlisle 1985; but see Colemann et al. 1985, for less clear results). Similarly, merlin females responded to brood size manipulations by investing more in nest defence when rearing larger broods. Brood size appears, thus, to be a determinant of offspring protection also in animals with biparental care. This may be more important among females than males, as suggested from evidence of nest defense being independent of brood size among males (Wiklund, in press).

Curio (1987) proposed that parental effort in feeding young would provide the parent with a rough estimate of the brood size. If parents use such a mechanism to perceive the number of young, a certain amount of time would probably be needed to respond to changes in brood size. In Experiment II, using manipulated brood sizes, the variation in nest defense during the second set of trials indicated that some females did not perceive the right size of their broods. Possibly, the responses might have been less variable with a longer time span between brood size manipulations and trials.

Dawkins and Carlisle (1976) proposed that the parent's prospects of fitness determines investment in parental care. Yet, tests of the hypothesis have not yielded conclusive evidence (Robertson and

Biermann 1979; Dawkins and Brockmann 1980; Carlisle 1985). One problem is that when prospects of fitness are measured by brood size, it is assumed that more young survive to breeding age from large broods than from small broods. The recruitment of young to local populations is related also to fledging date, in that proportionally more young are recruited from early than late broods (Newton 1986; Village, personal communication) – presumably, because young from early broods survive better than young from late ones (Newton 1986). In the merlins, survival of young of replacement broods may be reduced compared to that of young of first broods, as they reach fledging age about 2 weeks earlier (Wiklund, unpublished data).

In Experiment III, the defense intensity of seven females was examined twice during the same breeding season, i.e., once during the laying period of the first clutch and the next time at hatch of the replacement brood. With one exception, the latter category of broods was not defended as vigorously as first broods. This result did not verify a prediction of earlier studies, which suggests a positive correlation between nest defence intensity and age of young (e.g., Andersson et al. 1980; Biermann and Robertson 1981). Such a correlation has been obtained also among merlin females tending first broods (Wiklund, in press). Hence, age of young may not affect, in the same way, defense of replacement broods as it does the defense of first ones. Moreover, higher defense intensity at the first compared to the second exposure is not a characteristic effect of habituation, which seems to be associated with an increase in defense intensity (Knight and Temple 1986). Therefore, I presume that female offspring protection is related to brood size as well as to the prospects of producing young that reach reproductive age.

Brood size could be correlated with other factors, which would affect, in the same way, female nest defense. Yet, there is no evidence that investment in nest defense depends on body size (Wallin 1987; this study). Newton (1985) found, however, that lifetime reproductive success is higher among large compared to small females. An indirect effect of size on nest defense seems plausible, although it may contribute less to the variability in nest defense than do brood size and probability of chick survival.

There is an association between brood size and foraging success in that well-fed females have larger broods than other females (Newton 1986). Moreover, theoretical arguments suggest a relationship between the parent's foraging success/con-

dition and the amount of care given to the young (Carlisle 1982). In a study of tawny owl *Strix aluco* females, Wallin (1987) showed positive correlations between defense intensity and the parent's weight and condition, respectively. The defense behavior of merlin females, by contrast, seemed to be independent of body mass and condition. It is possible that traits such as size, weight, and condition may not directly affect nest defense but be underlying variables correlated with brood size. It is therefore necessary to uncouple these variables from brood size and separately examine each one of them before inferences can be made.

Theory predicts an increase in nest defense intensity with age of the parent (Carlisle 1982; Curio et al. 1984). Such a relationship has been indicated in one study only (Pugesek 1983); two other studies could not verify this relationship (Wallin 1987; Breitwisch 1988). Another example of age independent nest defense may be presented by merlin females, as there is no evidence of consistently increasing defense intensity with age (Wiklund, unpublished data).

The adaptive significance of nest defence

If level of investment depends mainly on net future benefits (Dawkins and Carlisle 1976), a positive correlation between investment level and reproductive success should occur. Such a relationship has been obtained in previous studies (Blancher and Robertson 1982; Wallin 1987) as well as in this one. The non-attacking merlin females produced less fledglings for two reasons: brood sizes were smaller, and chick losses were more frequent. Presumably, small brood sizes restrained investment in parental care, resulting in further reduction of the broods due to predation. Except for one case of starvation, chick losses were not recorded among attacking females. Hence, reduced impact of nest predators appears to be one advantage of female offspring protection.

Mobbing of predators is associated with certain risks, as retaliatory assaults by the predator could be fatal (e.g. Denson 1979; Ullman 1982; Buitron 1983; Walter 1983). In the tawny owl, females with high investment in nest defense seem to have shorter future lifetime than other females (Wallin 1987). Survival during nest defense might therefore be an important constraint on defense intensity. Given this, the prospective fitness gains at stake – e.g., the number of young surviving to independence – should be high enough to cancel the costs associated with the increased mortality risks before individuals pursue an unusually risky defense action.

Acknowledgements. I thank R. Dawkins, I. Newton, R.J. Robertson, W.J. Sutherland and A. Village for valuable comments on the manuscript, and B. Arvidsson, M. Asplund, M. Bjerhem, E. Isaksson, Y. Rydh and O. Winberg for assistance in the field studies. I am also indebted to the Swedish National Board of Environmental Protection for supporting the studies in Padjelanta and to AB Fiskflyg for an excellent travelling service. This study received economic support from the Swedish Natural Science Research Council (B-PD 8525-103), the Royal Swedish Academy for Sciences, the Royal and Hvitfeldtian Foundation, the Association of Royal Patriots and funds of the University of Gothenburg.

References

- Andersson M, Norberg RA (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 CG, Rundgren H (1980) Parental defence of offspring; a model and an example. *Anim Behav* 28:536–542
- Biebach H (1981) Energetic costs of incubation on different clutch sizes in starlings. *Ardea* 69:141–142
- Biermann GC, Robertson RJ (1981) An increase in parental investment during the breeding season. *Anim Behav* 29:487–489
- Blancher PJ, Robertson RJ (1982) Kingbird aggression: does it deter predation? *Anim Behav* 30:929–930
- Bradley JV (1968) Distribution-free statistical tests. Prentice-Hall, Englewood Cliffs, New Jersey
- Breitwisch R (1988) Sex differences in defence of eggs and nestlings by northern mockingbirds, *Mimus polyglottos*. *Anim Behav* 36:62–72
- Buitron D (1983) Variability in the responses of Black-billed magpies to natural predators. *Behaviour* 87:209–236
- Carlisle TR (1985) Parental responses to brood size in a cichlid fish. *Anim Behav* 33:234–238
- Carlisle TR (1982) Brood success in variable environments: implications for parental care allocation. *Anim Behav* 30:824–836
- Colemann RM, Gross MR, Sargent RC (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, 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
- Dawkins R, Brockmann HJ (1980) Do digger Wasps commit the Concorde fallacy? *Anim Behav* 28:892–896
- Dawkins R, Carlisle TR (1976) Parental investment, mate desertion and a fallacy. *Nature* 262:131–133
- Denson RD (1979) Owl predation on mobbing crow. *The Wilson Bulletin* 93:133
- East M (1981) Aspects of courtship and parental care in european robin *Erithacus rubecula*. *Ornis Scand* 12:230–239
- Greig-Smith PW (1980) Parental investment in nest defence by stonechats (*Saxicola torquata*). *Anim Behav* 28:604–619
- Haftorn S, Reinertsen RE (1985) The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). *Auk* 102:470–487
- Knight RL, Temple SA (1986) Why does intensity of avian nest defence increase during the nesting cycle? *Auk* 103:318–327

- Maynard Smith J (1977) Parental investment: a prospective analysis. *Anim Behav* 25:1–9
- Meijer T (1988) Reproductive decisions in the kestrel *Falco tinnunculus*. Phd thesis, University of Groningen, Groningen
- Newton I (1979) Population ecology of raptors. Poyser, Berkhamstead
- Newton I (1985) Lifetime reproductive output of female sparrowhawks. *J Anim Ecol* 54:241–253
- Newton I (1986) The Sparrowhawk. T & AD Poyser, Calton
- Newton I, Marquiss M (1984) Seasonal trend in the breeding performance of sparrowhawks. *J Anim Ecol* 53:809–829
- Pugesek BH (1983) The relationship between parental age and reproductive effort in the California Gull (*Larus californicus*). *Behav Ecol Sociobiol* 13:161–171
- Robertson RJ, Biermann GC (1979) Parental investment strategies determined by expected benefits. *Z Tierpsychol* 50:124–128
- Siegel S (1956) Non-parametric statistics for the Behavioural Sciences. McGraw-Hill, Tokyo
- Sokal RR, Rohlf FJ (1981) Biometry. WH Freeman and Company, New York
- Svensson L (1975) Identification guide to European passerines. Bonniers, Stockholm
- Taylor PS (1975) Breeding behaviour of the Snowy Owl. *The Living Bird* 12:137–154
- Ullman M (1982) White-tailed eagle, *Haliaeetus albicilla*, catching hooded crow, *Corvus corone*, in the air. *Var Fagelvarid* 41:337–338
- 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 PJ (1982) Risk-taking by red-winged blackbirds and the Concorde fallacy. *Z Tierpsychol* 60:199–208
- Wiklund CG (1979) Increased breeding success for merlins *Falco columbarius* nesting among colonies of Fieldfares *Turdus pilaris*. *Ibis* 121:109–111
- Windt W, Curio E (1986) Clutch defence in Great Tit (*Parus major*) pairs and the Concorde fallacy. *Ethology* 72:236–242