ORIGINAL PAPER

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Correlation between two components of parental investment: nest defence intensity and nestling provisioning effort of willow tits

Abstract Nest defence intensity and nestling provisioning effort of female willow tits (*Parus montanus*) were significantly correlated at the end of nestling period: well-fed young were defended most intensely. Increased effort was rewarded, since broods with the highest female per-offspring provisioning rates were the most likely to produce local recruits. This suggests that the feeding ability is an important cue for parental investment decisions, at least in a species like the willow tit which has adopted the clutch adjustment strategy. Thus, the most valuable broods would not necessarily be the largest ones, but the ones in which the original number of young could be fed most adequately. However, no associations were found between the level of parental effort and offspring weight, size or condition, nor did the broods producing recruits differ from other broods in timing of breeding or number and size of offspring. The female behaviour may suggest that they invest the most time, energy and risk in the young whose chances of joining the winter flock are the best. The first well-fed young also gain an advantage of prior residency in joining the flock. The first to join normally obtain higher social status, and hence better winter survival, than latecomers. The corresponding patterns in male parental investment behaviour were weak or absent, which suggested that the male effort was affected by the female behaviour. Males seemed to invest in nestling provisioning in such a way as to supplement the female effort. During nest defence action males also seemed to invest in protection of females against predation.

Key words Parental investment · Nest defence · Nestling provisioning · Feeding ability · *Parus* spp.

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Introduction

Trivers (1972) defined parental investment (PI) as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". The hypothesis of optimal PI assumes that natural selection operates primarily on investment (Morris 1987) and that the behavioural decisions involved in reproduction (e.g. clutch size) or parental care (e.g. nestling feeding, brood defence) are mechanisms which optimize this investment. Parents may differ (spatially and/or temporally) in the amount of resources they have to allocate in reproduction. On the other hand, an experienced or a reproductively efficient parent may be able to provide a higher reproductive effort with little or no additional physiological, survival or reproductive cost (e.g. Lessells 1991). Both phenotypic and genetic variation may result in individual differences in the level of optimal PI. Consequently, parents should also optimize the PI mechanisms by which they can maximize their lifetime reproductive success. Therefore, parents which can allocate more resources to reproduction, rather than parents which invest less in it, should have larger broods and invest more effort in different elements of parental care, provided that these are not constrained by each other.

Parental decisions involved in reproductive investment are prospective, i.e. they are based on the cost/benefit analyses of parental survival and future reproduction as a function of that investment (Maynard Smith 1977; Morris 1987). However, only in stable environments can birds adjust their PI level to forthcoming resource levels (e.g. clutch adjustment strategy, see O'Connor 1978). Still, even good predictions do not always hold, i.e. cost/benefit ratios change. Predictions which are too optimistic may result in brood reductions (O'Connor 1978) and/or lower

growth rates of the young (Fretwell et al. 1974; O'Connor 1978), which both presumably reduce the offspring fitness value. This would mean that the ability to feed the young adequately can be an important cue for the parents in their PI cost/benefit analyses. Thus, the most valuable broods may not necessarily be the largest ones, but those in which offspring requirements can best be satisfied (see also Gustafsson 1990).

Here we study the relations of two elements of parental care in willow tits: nestling feeding and brood defence. In willow tits both the parents feed the young (Rytkönen et al. 1993, 1995) and defend the nest against predators (Rytkönen et al. 1990, 1993). Nestling feeding behaviour is obviously the most costly element of parental care (e.g. Martin 1992). The direct costs are realized in energy and time expenditure which may later cause increased starvation and predation risk. Brood defence may not be energetically very costly, but it can be fatally risky (Curio and Regelman 1985). Because they have different instant costs these two elements may not constrain each other (Ricklefs 1984; but see Martin 1992). If this is true, we can expect both these elements to be correlated with the parental investment level and thus with each other. Orell and Ojanen (1983a) showed that willow tits have adopted a clutch adjustment strategy (O'Connor 1978). We would then expect that the better the parents succeed in their resource level predictions, i.e. the better they can satisfy the needs of their offspring, the more these parents are willing to invest time, energy and risk in their young. As a result, we should find a correlation between per-offspring feeding effort and brood defence intensity, which in turn should both be connected with offspring fitness value.

Methods

Study area, species and population

This study was conducted near Oulu in northern Finland (65°N,25°30'E) in 1990–1991. The study area consists of mixed deciduous and coniferous forests (see Orell and Ojanen 1983a, b). The willow tit (*Parus montanus*) is a small monogamous and territorial passerine (body mass 12 g). The population studied is colour-banded, and thus the similar-looking sexes could be distinguished. Some of the broods studied here were size-manipulated (reduced and enlarged by two chicks, in detail see Orell and Koivula 1988, 1990), but earlier studies showed that those manipulations *per se* had no effect on the per-offspring feeding performance. Nevertheless, parents provided for their young as would have been predicted from the actual brood size (Rytkönen et al., unpublished work). Likewise, brood size manipulations did not affect brood defence (Rytkönen et al. 1995). Therefore, we think that this study was not affected by brood size manipulation.

Ecological and biometrical measurements

Standard methods were used in collecting the breeding biology data (Orell and Ojanen 1983a, b) and in biometrical measurements of the birds (body mass; wing, tail and tarsus lengths; see Orell and Koivula 1988). The condition index was derived as the residuals of

weight in a linear regression of weight on tarsus length (see Linden 1988). The nest age was counted as days from the initiation of egg laying. Brood size refers to the actual brood size at respective nestling stage. Recruitment was considered in means of local recruitment, i.e. those young that survived till the subsequent breeding season and settled on our study area. Because of high site tenacity, mortality could reliably be measured as the disappearance of adult birds from their territories (Orell and Koivula 1988).

Nestling feeding measurements and variables

Video monitoring was used for measuring the sex-specific provision rates and load sizes at 24 and 21 nests in 1990 and 1991, respectively. A camouflaged video-camera on a tripod was placed 2–3 m from the nest. Samples of 1.5 h were recorded during the first and the latter half of the nestling period when the age of nestlings was about 5 and 11 days, respectively. The recordings were made between 8 a.m. and 6 p.m. when parental activity stayed constantly high (Rytkönen et al., unpublished work). Sexes were distinguished by the colour rings, and load sizes were estimated in relation to the bill length using a scale from 1 (smallest) to 9 (largest loads). The size measurements were corrected to fit linearity by empirically studying the relationship between size measurements and weights of artificial loads. A curvilinear regression model showed that the relative accuracy of the corrected values was 92%. These were only relative measures for the load sizes; however, by using the corrected linear scale, we could also estimate a relative value for total feeding effort of each parent by multiplying visiting rate by the corrected load size. In addition, we measured the daily visiting rates during the nestling period by using an automatic visits recorder set (manufactured by CortexT GM, Hungary). This device did not separate sex-specific visits, but was useful when testing whether the video samples described the overall feeding rates.

The variables describing the sex-specific provisioning behaviour were (1) visiting rate (VR) as visits per hour, (2) load size (LS) and (3) total feeding effort (FE), which gives a relative measure for the total amount of food delivered per hour (FE = VR × LS). Since per-offspring effort was dependent on brood size (i.e. provisioning is depreciable care, see Lazarus and Inglis 1986; Clutton-Brock and Godfray 1991; Rytkönen et al., unpublished work), relative per-offspring efforts were derived as the residuals of per-offspring visiting rate (VR) and total feeding effort (FE) in the multiplicative regression (model $y = ax^b$, $b < 0$) of per-offspring VR and FE on brood size.

Nest defence trials and variables

Nest defence trials were carried out at the beginning and end of nestling period. The first trials were done on different days from the video recordings, but the second trials just after the video recordings ended. In 1991 an additional third defence trial series was conducted just after the first video recording. Defence behaviour against a mounted stoat (*Mustela erminea*) was measured. At a trial the predator model was placed 25 cm below the nest entrance. The distances of male and female parent from the model were continuously determined during a 5-min period. The alarm calls of the birds were also recorded (on C-casettes). The method is described in detail in Rytkönen et al. (1990, 1993).

The recordings were analysed later (computer aided), and the nest defence behaviour was described by four variables: (1) the average (= mean) (AD) and (2) the minimum approach distance (MD) of the parent from the predator model; (3) the alarm calling rate (calls/min) during the trial (CR); and (4) the mobbing behaviour: birds were scored as mobbers or non-mobbers. Birds diving and striking the predator model were classified as mobbers (see Knight and Temple 1986). We assume that the parent bird took a greater risk the nearer it stayed or visited the predator model, and

Table 1 Pearson correlation coefficients (*r*) between nest defence intensity at the end of nestling period (*AD* average approach distance, *MD* minimum approach distance, *CR* calling rate) and independent variables describing (a) provisioning effort per-brood and per-offspring and (b) brood value. Sample sizes for females are 32–35 broods, and for males 27–30 broods

Independent variable	Females			Males		
	AD	MD	CR	AD	MD	CR
(a) provisioning variables:						
Visiting rate (VR)	−0.43*	−0.46**	−0.07	−0.18	−0.28	−0.14
Per-offspring VR	−0.57***	−0.49**	0.02	−0.27	−0.24	−0.14
Load size (LS)	0.12	0.10	−0.17	0.33	0.39*	0.11
Per-offspring LS	−0.03	0.06	0.05	0.17	0.42*	0.24
Feeding effort (FE[a])	−0.36*	−0.39*	−0.15	0.06	−0.03	−0.14
Per-offspring FE	−0.48**	−0.38*	−0.08	0.02	0.06	−0.06
(b) brood value variables:						
Clutch size	0.09	0.03	−0.03	0.24	0.26	−0.14
Brood size	0.03	−0.17	0.05	0.21	−0.18	−0.13
% Surviving young	−0.03	0.16	−0.06	−0.17	0.26	0.10
No. Dead young	0.01	0.20	−0.07	−0.11	0.30	0.07
Timing of breeding	0.10	0.25	0.04	0.27	0.00	0.26
Nestling weight	0.07	0.14	−0.17	0.03	0.28	0.36*

[a] FE = VR × LS
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

the more alarm calls it gave. Mobbing was considered the most risky behaviour.

Results

Female behaviour

Average and minimum approach distances of female parents correlated negatively with per-brood and per-offspring provisioning effort (visiting rate and total feeding effort) (Table 1a, Fig. 1). This indicates that females that invested most in provisioning their young

Fig. 1 The relationships between female nest defence intensity (average and minimum approach distances) and relative per-offspring provisioning effort (visiting rate; feeding effort = visiting rate × load size, see Methods). Linear regression slopes for each correlation are presented. Statistics are presented in Table 1a
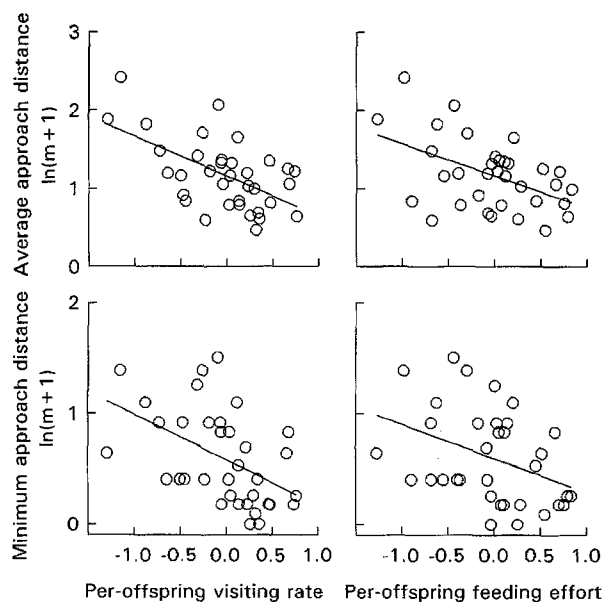
defended their broods most intensely at the end of nestling period. On the other hand, alarm calling rates were not related to nestling provisioning effort (Table 1a). At the beginning of the nestling period no significant correlations between brood defence intensity and nestling provisioning effort were found ($|r| < 0.227$, $n = 33$, all $P > 0.20$). The first video recordings were conducted on different days from defence trials, thus differing from the method used at the end of nestling period. In 1991 we therefore conducted an additional series of recordings just after the first defence trials. Still no significant relationships between defence intensity and provisioning effort at the beginning of nestling period were found (all $|r| < 0.242$, $n = 14$, all $P > 0.40$).

The significant correlations between defence intensity and provisioning effort were not explained by temporarily varying motivation levels for parental care. Hourly visiting rates and total feeding efforts, based on 1.5-h video recordings, correlated significantly with the overall daily visiting rates during the latter half of nestling period (days 8–13) ($r = 0.424$–0.643, $n = 27$–28, all $P < 0.025$; for valid analyses, only the broods in which both parents were found to feed were included here).

Male behaviour

In contrast to results for females, male nest defence intensity did not correlate with visiting rates or total feeding effort (Table 1a). At the end of nestling period, however, males that brought the largest food loads for their young underwent the lowest risks in brood defence, as measured by minimum approach distances (Table 1a). On the other hand, males that brought the smallest loads (and defended their broods most intensely, as pointed out above) visited their nests most frequently ($r = -0.423$, $n = 31$, $P = 0.018$).

Parental interactions

At the beginning of the nestling period both per-brood and per-offspring total feeding efforts of male and female parents were positively correlated ($r = 0.410$ and 0.427, both $n = 31$, $P = 0.020$ and 0.017, respectively). Visiting rates and load sizes showed similar non-significant positive relationships (all $P > 0.10$). At the end of the nestling period male and female behaviour was independent, with a slight tendency towards a reversed relationship, as revealed by non-significant inter-sexual correlations in per-brood ($-0.235 < r < 0.253$, $n = 26$–30, all $P > 0.20$) and per-offspring total feeding efforts ($-0.347 < r < -0.046$, $n = 28$–30, all $P > 0.07$).

PI behaviour and offspring fitness value

Figure 2 presents the association between provisioning effort and offspring fitness value. The broods which produced local recruits were characterized by significantly higher female per-offspring provisioning effort at the end of nestling period as compared with unsuccessful broods. Logit models (NAG 1986) revealed that only per-offspring total feeding effort (change in deviance 4.42, $df = 1$, $P < 0.05$) could significantly explain the variation in local recruitment, whereas no effect of variables describing brood value (see Table 1b) was found (changes in deviance < 0.74, $df = 1$, $P > 0.10$). Recruitment was also independent of male or pooled male and female provisioning effort (changes in deviance < 1.01, $df = 1$, $P > 0.10$). Actually, male effort in successful broods was lower than in unsuccessful broods. Nest defence intensity of the parents tending broods producing and not producing recruits was equal in both sexes (t-tests, all $P > 0.20$).

Fig. 2 The relationships between local recruitment and female per-offspring feeding effort. Broods producing local recruits were characterized with suggestively ($t = 1.84$, $P = 0.074$) higher per-offspring effort at the beginning and significantly ($t = 2.05$, $P = 0.048$) higher per-offspring effort at the end of nestling period than broods failing to produce local recruits. Sample sizes are given for each bar
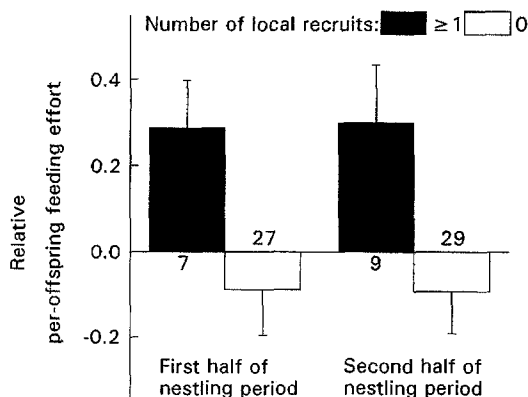
No connections between offspring fitness value and defence intensity were detected during the nestling period, except for one between mean nestling weight and calling rate of males (Table 1b). This exception, which was opposite to the prediction of PI theory, did not emphasise any existing trends in the data. The weight, condition and size (wing, tail and tarsus length) of the 13-day-old nestlings did not correlate with the per-brood or per-offspring visiting rate or total feeding effort ($-0.267 < r < 0.104$, $n = 31$–39, all $P > 0.10$). High provisioning effort was not connected with early breeding either ($|r| < 0.194$, $n = 31$–39, all $P > 0.20$). On the other hand, the variation in offspring quality was very low: e.g. for mean offspring weight CV $= 7.7\%$. This probably indicates that offspring weight was optimized to certain level, not maximized, and thus the interpretation of the correlation results may actually be impossible.

Costs of provisioning

The higher provisioning effort of the female parents producing local recruits seemed to have no survival or condition costs. There were no significant mortality differences between the parents producing and not producing local recruits (Fisher exact test, 2-tailed $P > 0.10$). Actually, survival of the successful parents (89% for both sexes; $n = 9$) till the next breeding season seemed to be better than that of the others (62% and 59% for females and males, respectively; $n = 34$). Furthermore, the successful females tended to be heavier and in better condition than the unsuccessful females at the end of nestling period ($t = 1.75$ and 1.74, both $n = 9 + 27$, $P = 0.089$ and 0.090, respectively). However, no corresponding difference was detected in tarsus length ($t = 0.69$, $P > 0.40$).

The above relationships may suggest that only the high-quality females could feed their young properly. In contradiction to this, female provisioning effort was not associated with condition or weight (all $|r| < 0.122$, $n = 34$–37, $P > 0.490$). On the other hand, female condition might positively affect her nest defence intensity, since female minimum approach distances correlated significantly with condition ($r = -0.412$, $n = 35$, $P = 0.014$) and weight ($r = -0.390$, $n = 35$, $P = 0.021$). However, no corresponding relationship was found for the other female defence variables or in any of the male data (all $P > 0.151$).

Discussion

Two elements of parental care, nest defence intensity and nestling feeding effort, showed a significant positive correlation in female willow tits. Those females that invested the most energy and time in feeding their young underwent the riskiest nest defence behaviour. The significance of this result rests on two main arguments.

First, this relationship was not due to temporarily varying motivation for parental care, but probably reflected the costs and benefits of parental investment behaviour. Second, by using per-offspring provisioning rates, the comparison of these elements was on a correct basis, because it took into account the basic difference of these two parental care types. Nest defence is *non-depreciable* care, because all the young benefit simultaneously and equally from a unit of PI, and nestling provisioning is *depreciable* care, because each offspring benefits independently and benefits decline with increasing brood size (e.g. Clutton-Brock and Godfray 1991; see also Lazarus and Inglis 1986).

PI behaviour and offspring fitness value

Female provisioning effort and nest defence intensity indicated similar willingness to invest in the offspring. The connection between nestling provisioning effort and recruitment show that high PI level was rewarded (see Fig. 2). This result suggests that the most valuable broods are not necessarily the largest ones, but those in which the nestlings can be fed most adequately. Hence, the ability to feed the current young would be an important cue for the PI decisions. On the other hand, the results based on local recruitment rate are always critical. One could argue that less-fed broods produced recruits that were not found in our study area. There were, however, no differences in timing of breeding, brood size and offspring size between well-fed and poorly fed broods (by females), which would suggest that expected dispersal distances should not differ either (e.g. Greenwood 1980). High per-offspring feeding effort may also reflect rich food resources during the post-fledging period and thus, function as a cue for better expected juvenile survival.

Higher female defence intensity for well-fed offspring is understandable since those offspring proved to have better chances of recruiting. There is evidence for the assumption that different allocation of investment in nestling provisioning or nest defence affect offspring survival. Heavy nestlings survive best in many passerines (e.g. Perrins 1965; Nur 1984; for review see Magrath 1991). High nest defence intensity has been found to be connected with increased survival of the brood (e.g. Greig-Smith 1980; Blancher and Robertson 1982; for review see Martin 1992). Against the prediction, we did not find any relationships between the female effort and the factors describing the offspring fitness value (nestling size, weight or condition; see Winkler 1987; Montgomerie and Weatherhead 1988). However, this may be explained by the fact that males tended to decrease their provisioning effort when females increased it, thus diminishing the between-brood differences. Hence, nestling weight was optimized rather than maximized (see also Nur 1984), which was also proved by the low variation in nestling weight. In willow tits nestling weight optimization may function so long as parents do not jeopardise their own survival (see below). Nevertheless, this would not clarify those offspring characteristics which would secure a better survival for the well-fed young than for the others.

A mechanism that could possibly explain the success of the well-fed young is associated with the social organisation of the willow tits. Outside the breeding season, willow tits live in stable-structured flocks consisting normally of an old pair and one or two young pairs (Koivula and Orell 1988). As a rule, old birds are dominant over young birds and males over females, with the social hierarchy being linear in the flock (Koivula and Orell 1988). The social status of a bird is positively associated with winter survival (Ekman and Askenmo 1984; Hogstad 1988; Koivula and Orell 1988). The order in which the young birds join the flock after fledging is correlated with the social status of the joiners: the first-settling birds normally dominate the late-comers (Hogstad 1990). The latest fledgings may not even get a winter territory at all, and the survival prospects of these "floaters" are quite desperate (Hogstad 1990). This so called advantage of prior residency has also been demonstrated in laboratory experiments (Koivula et al. 1993). Because of prior residency, early breeding (see Smith 1993) and fast growth rate (Ricklefs 1984) would therefore be beneficial for willow tits. These two factors, however, cannot be maximized: the abundance of the most profitable prey, caterpillars, increases during the course of the breeding season and peaks when the latest broods are fledging (Rytkönen et al., unpublished work). By feeding the young with caterpillars parents can bring the largest amount of food per time unit (Rytkönen et al., unpublished work). Willow tits, however, breed before they can take a full advantage of the caterpillar peak. For comparison, local great tits (*Parus major*) breed 1–2 weeks later than willow tits (Orell and Ojanen 1983b), and thus their hatching matches the caterpillar peak better. As a result, the fittest willow tit offspring would be produced by those broods which were both initiated early and could first be fed adequately. Therefore, the most valuable broods normally are those laid in the middle of the willow tit's breeding season. This is in accordance with our finding that female parents defend middle-season broods most intensely (Rytkönen et al. 1995). Thus, the variation in female PI behaviour suggests that females allocate most energy, time and risk to broods which can first be fed adequately, and which will most probably produce local recruits, perhaps due to their offspring's prior residency advantage in joining the winter flocks.

The costs of parental investment

PI theory would predict that parents with good offspring survival prospects should invest more of their

own resources in their young (Montgomerie and Weatherhead 1988). However, the variation in provisioning effort did not support this prediction: the parents that succeeded in producing recruits did not suffer higher condition or survival costs than the unsuccessful parents. Alternatively, the correlation between female defence intensity and provisioning effort could suggest that only the fittest females are able to both feed the young properly and defend these vigorously. This, however, seemed not to be the explanation for the above correlation, since high female feeding effort was not associated with good condition or heavy weight. The variation in minimum approach distances might suggest that the fittest and heaviest females tended to be the most vigorous defenders (see also Rytkönen et al. 1993), but this is not necessarily an indication of higher PI level, since a fit bird can engage in more intense defence behaviour than a weak bird with the same risk (or cost) level (e.g. Montgomerie and Weatherhead 1988).

The independence of female condition and survival from her provisioning effort level might be related to the willow tits' ability to quite precisely adjust their clutch size to the forthcoming resource levels (the clutch adjustment strategy, see O'Connor 1978). In surviving broods 91% of the eggs produce fledglings (Orell and Ojanen 1983a). Brood size manipulation experiments have shown that the parental fitness (*sensu* Gustafsson 1985) through enlarged, natural and reduced broods is equal, suggesting that the costs of reproduction are almost independent of brood size (see also Orell and Koivula 1988, 1990). The lack of correlation between nest defence intensity and brood size suggests the same (see also Rytkönen et al. 1995). In accordance with this, brood size has been found to be a marginal component in explaining the variation of lifetime reproductive success in many small passerines (e.g. McCleery and Perrins 1988). The well-functioning clutch adjustment strategy may also explain why defence intensity was not affected by the number or proportion of dead nestlings: these are normally none or few.

Though the clutch adjustment strategy (O'Connor 1978) works well in willow tits, predictions can never succeed perfectly. Therefore, later, further PI adjustment would be advantageous. According to the PI theory, brood size is one mechanism by which parents optimize their lifetime reproductive success (Morris 1987). Clutch size can be considered the original PI decision. As mentioned above, nestling provisioning ability would be more reliable cue for the expected brood success than the brood size and therefore, the later adjustment of PI could be independent of brood size. The guide-line in this later PI adjustment seems to be the avoidance of condition or survival costs (see Gustafsson 1990). The brood size manipulation experiments have shown that in enlarged broods (by 30% above the normal size) parents try to secure their own survival rather than their offspring's survival (Orell and

Koivula 1988, 1990; see also Stearns 1992). The suggested mechanism for this is based on the trade-off between parental condition and offspring needs, which results in increased per-brood provisioning effort but decreased per-offspring effort with increasing brood size (Nur 1984; Conrad and Robertson 1993; Rytkönen et al., unpublished work). When food resources are limited, parents must reduce per-offspring effort to avoid condition costs, but when resources remain sufficient, per-offspring effort can be kept adequate or increased without extra costs to parental condition.

Sexual differences and interactions

Male provisioning effort did not show a similar relationship with nest defence intensity to that of the females. By contrast the most aggressive males brought the smallest food loads for their young. On the other hand, the smallest loads were brought by the most frequently feeding males. Thus, the slight tendency for the most frequently visiting males to undergo higher risks while defending the nest might have some behavioural significance comparable to that found among females, particularly if frequent visiting at the nest is considered as nest guarding behaviour (see below).

The sexual differences in the results of this study may be connected with sexual differences in each PI behaviour type. At the end of nestling period males are more vigorous defenders than females (Rytkönen et al. 1993). However, females visit the nest slightly more frequently, but bring significantly smaller loads than males do (Rytkönen et al., unpublished work). The dynamics of how the parents share the risk of defence may also affect PI decisions (Rytkönen et al. 1993). The higher male defence intensity and direct observations suggest that males protect their mates during the defence action. Males sometimes perch between the predator model and female and occasionally males even push the female away by attacking her. This phenomenon seems to be parallel to that found in willow tit winter flocks in which dominant males protect their mates (Ekman 1990; Hogstad 1995). The protected females use safer feeding places and suffer lower mortality during winter as would be predicted from their rank (Ekman 1990; see also Koivula et al. 1994). This protection by males may constrain male defence behaviour in such a way that no female-like relationships between defence intensity and provisioning effort can be found. The "better" responses found in females may also be explained by the finding that in many tit species breeding parameters are mainly determined by the properties of females (Slagsvold and Lifjeld 1990; see also Orell et al. 1994) i.e. females seem to be better aware of what is going on.

The PI effort level may also affect sexual differences in the relationships between provisioning effort and nest defence intensity. Winkler's general model for parental

care (Winkler 1987) predicts that mate effort would affect the focal parents' PI behaviour. At a low effort level the parents' behaviour is expected to inter-correlate positively (Winkler 1987). In willow tits the positive correlation between male and female provisioning effort in the beginning of nestling period support this prediction. At a high effort level, in which the costs of behaviour are realistic, the corresponding correlation is expected to be negative (Winkler 1987). We found only weak support for this at the end of nestling period. However, when parental provisioning efforts tend to correlate negatively at the end of nestling period, and the nest defence intensity of each pair is always positively inter-correlated (Rytkönen et al. 1993; suggesting that defence behaviour functions at a low effort level compared with nestling provisioning; see also Winkler 1991), this may actually preclude the other mate's predicted correlation between provisioning effort and nest defence intensity. The lacking correlation between male provisioning effort and nest defence intensity may thus be understandable. But why are males in this role? As presented above, breeding parameters of tits are mainly determined by female properties (Slagsvold and Lifjeld 1990) and, thus, females are probably always more "aware" of the brood value. Therefore, when the value of the brood is high, females will be willing to put more effort in provisioning it, while the contribution of the male may then automatically decrease. As a result, male provisioning effort seems to be independent of both the brood value and, consequently, of the willingness to invest in nest defence.

Male role and nest guarding

Martin (1992) considers nest guarding, i.e. perching near the nest, one of the most important avian antipredator strategies. In willow tits, however, nests cannot be guarded continuously since the territories are large, on the average of 10 ha (Orell and Ojanen 1983a). One possible guarding strategy for willow tits would be frequent visiting at the nest. Thus, the relationship between visiting rate and defence intensity in females could also be interpreted as a means of nest guarding. On the other hand, if frequent visiting is only a nest guarding strategy, this would indicate that females invest more than males in the safety of the brood at the end of the nestling period. This, however, conflicts with the pattern of brood defence in which males are more vigorous defenders (Rytkönen et al. 1993). Sexual differences in visiting rates might be explained better by sex-specific territory use (Rytkönen et al., unpublished work). If males forage further away from the nest, according to the central-place foraging model (Orians and Pearson 1979) optimal male round-trip travel time would be longer and load size larger than those of females. However, within each sex, the feed-

ing strategy of those birds that invest most in guarding and defending the nest would be more frequent visiting with a lesser load size, provided that the young are also adequately fed by this strategy. In this light, the negative correlation between male defence intensity and load size would indicate such a nest guarding strategy, and thus patterns in male PI behaviour are to some extent comparable with those of females. In high-quality broods, where females invest most in provisioning and defending the nest and thus reduce the male contribution to provisioning, males would be able to invest more in nest guarding, i.e. frequent visiting, which would then explain their smaller loads.

References

Blancher PJ, Robertson RJ (1982) Kingbird aggression: does it deter predation? Anim Behav 30: 929–930
Clutton-Brock T, Godfray C (1991) Parental investment. In: Krebs JR, Davies NB (eds) Behavioural ecology. An evolutionary approach. Blackwell, Oxford, pp 234–262
Conrad KF, Robertson JR (1993) Brood size and the cost of provisioning nestlings: interpreting Lack's hypothesis. Oecologia 96: 290–292
Curio E, Regelmann K (1985) The behavioural dynamics of great tit (*Parus major*) approaching a predator. Z Tierpsychol 69: 3–18
Ekman J (1990) Alliances in winter flocks of willow tits: effects of rank on survival and reproductive success in male-female associations. Behav Ecol Sociobiol 26: 239–245
Ekman J, Askenmo C (1984) Social rank and habitat use in willow tit groups. Anim Behav 32: 508–514
Fretwell SD, Bowen DE, Hespenheide HA (1974) Growth rates of young passerines and the flexibility of clutch size. Ecology 55: 907–909
Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28: 1140–1162
Greig-Smith PW (1980) Parental investment in nest defence by stonechats (*Saxicola torquata*). Anim Behav 28: 604–619
Gustafsson L (1985) Fitness factors in the collared flycatcher *Ficedula albicollis* Temm. Ph D Thesis, University of Uppsala
Gustafsson L (1990) Life-history trade-offs and optimal clutch size in relation to age in the collared flycatcher. In: Blondel J, Gosler A, Lebreton JD, McCleery R (eds) Population biology of passerine birds, an integrated approach (NATO ASI Ser G: Ecological Science 24). Springer, Berlin Heidelberg New York, pp 235–245
Hogstad O (1988) Rank-related recourse access in winter flocks of willow tit *Parus montanus*. Ornis Scand 19: 169–174
Hogstad O (1990) Dispersal date and settlement of juvenile willow tits *Parus montanus* in winter flocks. Fauna Norv Ser C Cinclus 13: 49–55
Hogstad O (1995) Alarm calling by willow tits, *Parus montanus*, as mate investment. Amin Behav 49: 221–225
Knight RL, Temple SA (1986) Methodological problems in studies of avian nest defence. Anim Behav 34: 561–566
Koivula K, Orell M (1988) Social rank and winter survival in the willow tit *Parus montanus*. Ornis Fenn 65: 114–120

Koivula K, Lahti K, Orell M, Rytkönen S (1993) Prior residency as a key determinant of social dominance in the willow tit *Parus montanus*. Behav Ecol Sociobiol 33: 283–287

Koivula K, Lahti K, Rytkönen S, Orell M (1994) Do subordinates expose themselves for predation: field experiments on feeding site selection of willow tits. J Avian Biol 25: 178–183

Lazarus J, Inglis IR (1986) Shared and unshared parental investment, parent-offspring conflict and brood size. Anim Behav 34: 1791–1804

Lessells CM (1991) The evolution of life-histories. In: Krebs JR, Davies NB (eds) Behavioural ecology. An evolutionary approach. Blackwell, Oxford, pp 32–68

Linden M (1988) Reproductive trade-off between first and second clutches in the great tit *Parus major*: an experimental study. Oikos 51: 285–290

Magrath RD (1991) Nestling weight and juvenile survival in the blackbird, *Turdus merula*. J Anim Ecol 60: 335–351

Martin TE (1992) Interaction of nest predation and food limitation in reproductive strategies. Curr Ornithol 9: 163–197

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

McCleery RH, Perrins CM (1988) Lifetime reproductive success of the great tit *Parus major*. In: Clutton-Brock TH (ed) Reproductive success. University of Chigago Press, London, pp 136–153

Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defence by parent birds. Q Rev Biol 63: 167–187

Morris WM (1987) Optimal allocation of parental investment. Oikos 49: 332–339

NAG (1986) The GLIM system release 3.77 manual. Numerical Algorithms Group, Oxford

Nur N (1984) Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. Oecologia 65: 125–137

O'Connor RJ (1978) Growth strategies in nestling passerines. Living Bird 16: 209–238

Orell M, Koivula K (1988) Cost of reproduction: parental survival and production of recruits in the willow tit *Parus montanus*. Oecologia 77: 423–432

Orell M, Koivula K (1990) Effects of brood size manipulations on adult and juvenile survival and future fecundity in the willow tit. In: Blondel J, Gosler A, Lebreton JD, McCleery R (eds) Population biology of passerine birds, an integrated approach. (NATO ASI Ser G: Ecological Science 24). Springer, Berlin Heidelberg New York, pp 297–306

Orell M, Ojanen M (1983a) Breeding biology and population dynamics of the willow tit *Parus montanus*. Ann Zool Fenn 20: 90–114

Orell M, Ojanen M (1983b) Timing and length of the breeding season of the great tit, *Parus major*, and the willow tit, *P. montanus*, near Oulu, northern Finland. Ardea 71: 183–198

Orell M, Koivula K, Rytkönen S, Lahti K (1994) To breed or not to breed: causes and implications of non-breeding habit in the willow tit *Parus montanus*. Oecologia 100: 339–346

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs CR (eds) Analysis of ecological systems. Ohio State University Press, Columbia, pp 154–177

Perrins CM (1965) Population fluctuations and clutch-size in the great tit, *Parus major* L. J Anim Ecol 34: 601–647

Ricklefs RE (1984) The optimization of growth rate in altricial birds. Ecology 65: 1602–1616

Rytkönen S, Koivula K, Orell M (1990) Temporal increase in nest defence intensity of the willow tit *Parus montanus*: parental investment or methodological artifact? Behav Ecol Sociobiol 27: 283–286

Rytkönen S, Orell M, Koivula K (1993) Sex-role reversal in willow tit nest defence. Behav Ecol Sociobiol 33: 275–282

Rytkönen S, Orell M, Koivula K (1995) Pseudo Concorde fallacy in the willow tit? Anim Behav 49: 1017–1028

Slagsvold T, Lifjeld JT (1990) Influence of male and female quality on clutch size in tits (*Parus spp.*). Ecology 71: 1258–1266

Smith HG (1993) Seasonal decline in clutch size of the marsh tit (*Parus palustris*) in relation to date-specific survival of offspring. Auk 110: 889–899

Stearns SC (1992) The evolution of life histories, 1st edn. Oxford University Press, Oxford

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B(ed) Sexual selection and the descent of man. Aldine Publishing Company, Chicago, pp 136–179

Winkler DW (1987) A general model for parental care. Am Nat 130: 526–543

Winkler DW (1991) Parental investment decision rules in tree swallows: parental defence, abandonment, and the so-called Concorde fallacy. Behav Ecol 2: 133–142