Determinants of brood defence in the great tit *Parus major* L.

Klaus Regelmann and Eberhard Curio

Arbeitsgruppe für Verhaltensforschung, Abteilung Biologie, Ruhr-Universität Bochum, Postfach 102148, D-4630 Bochum, Federal Republic of Germany

Summary. Great tits (*Parus major*) tending nestlings reacted defensively to a live predator (*Glaucidium perlatum*; domestic cat) and the playback of a mixed species mobbing chorus, or to the latter alone. Defensive behaviour, mainly mobbing, reflected the risk taken and is assessed by five measures. Multivariate and contingency analyses revealed that at least 11 of 16 contextual independent variables affected the risk taken. Incremental effects are due to: Age of young, sex of the defending bird, the expected number of neighbouring mobbers, low temperature, wet canopy, the raptor's distance from cover, coniferous forest, advancing season. A decremental effect is exerted by a large brood that is older. Annual differences in defence arise probably from demographic factors such as fecundity, which in turn affect the parent's benefit-cost ratio (number of young of the same sex as the parent/residual reproductive value of the parent).

While the effects of annual fecundity, age of young and season were predicted on the basis of this benefit-cost ratio, the failure to verify an incremental effect of brood size runs counter to established theory. We conclude that parents gear their defence efforts to energy investment, past or future, and are mal-adapted to brood size as a promotor of risk taken. The influence of the habitat is poorly understood. At least three factors (age and number of young, parent's sex) act additively on part of the response. Despite the large number of variables examined, about 43% of the total response variance remains unexplained.

While four defence measures are determined by at least 10 contextual factors, a fifth measure, the male's minimum distance from the raptor, is determined by one other factor, the appearance of the ♀ mate. The latter leads us to assume an additional, social rôle of brood defence.

Risk-assessment by great tits leading to risk-aversive defence behaviour is governed by evolved *restraints* rather than by momentary *constraints*. Examples are provided by the effects of weather and cover.

Introduction

Animals must continually decide between various alternative behaviours in order to maximize their fitness. The severity of a decision depends on how much it affects the animal's fitness. For example, by deviating from its optimal daily feeding frequency by one feeding visit to its brood a bird would incur a smaller disadvantage than by defending it against a predator in the wrong way: with suboptimal risk taken by the parent the predator would not be dissuaded and might threaten the parents as well as their offspring; by risking too much, the defender would be killed (refs. in Curio 1978). The delicate balance which a defending parent has to strike between these extremes might be expected to leave little room for choosing between options. Yet the variation between pairs or mates of a pair of the great tit (*Parus major*) in the pattern of their defence behaviour is bewildering (Curio 1975, 1980).

We are led to ask three questions:
(1) What are the determinants of this variation and can they be meaningfully interpreted?
(2) Are all risk-related properties of the response affected by the same set of cues or by different ones? An answer to this question would help settle the problem whether the response serves one or more goals.

Being iteroparous, great tits embark on a new breeding attempt if the current one fails. However, as they are also short-lived their chances of doing

so are small (Perrins 1979; Curio and Regelmann 1982). Hence one would expect parent great tits to take considerable risks in defending their brood by mobbing a predator near the brood. This behaviour is directed at offspring protection and not (only) at self-defence since great tits (and blue tits *Parus caeruleus*) exhibit an acoustic anti-predator response only at their own nest, not at a neighbour's nest, where they remain silent (personal observation; Shalter 1979). Furthermore, strength of response increases with age of young, as in many other altricial birds (Curio 1975; Andersson et al. 1980; see also Shalter 1979: *Parus caeruleus*).

(3) Do parents assess the value as minored by the age of the brood by measuring past investment and future expected benefits? We will provide evidence that great tits do *not* invest in offspring on the basis of future offspring number, thus raising the question whether they commit the Concorde Fallacy.

From 1976 to 1980 we studied great tits in the wild with the objective of elucidating the processes and adaptations involved in learning to respond to owl calls (Curio et al. 1978). As a first and necessary step, determinants of brood defence will be interpreted within a coherent conceptual framework, notably one of cost-benefit consideration.

Methods and study areas

Experimental procedure

Pairs of great tits (*Parus major*) with nestlings were presented with a playback of a mixed-species mobbing chorus of six species (including the great tit, see Curio 1980) plus an artificial, pulsed 800-Hz tone with the loudspeaker juxtaposed either to a caged, live pigmy owl (*Glaucidium perlatum*) or to a live domestic cat of wild-type colouration positioned about 3 m in front of the nest box. In two 'predator-free' experiments the stimulus consisted of the playback alone. This time the loudspeaker was put on twigs 10–20 cm above ground and beamed upwards. For the rationale of the experiments see Curio et al. (1978). This mobbing chorus tape is a powerful lure for most European woodland songbirds (Fig. 1). The 6 min chorus playback was recorded from the start of a natural mobbing episode triggered by a stuffed European pigmy owl (*Glaucidium passerinum*). This sound stimulus was broadcast from a UHER stereo Report 4200 at 19 cm/s via a midfrequency speaker (details in Curio 1980). For SPL of the sound stimulus see p. 133.

Before the test, the predator was mounted in its covered cage 1.5 m above ground at the top of a bamboo pole during a feeding interval. The cage was uncovered seconds before the start of the sound stimulus giving the experimenter time to withdraw without provoking untimely mobbing. Upon termination of the 8-min playback, the live predator was covered and removed along with its cage and the loudspeaker. The next day the birds were tested for learning with the novel sound stimulus (played alone for 2 min) followed by the taped mobbing chorus, representing the same 5 min of auditory stimulation that had previously concluded the conditioning sound stimulus (Fig. 1).
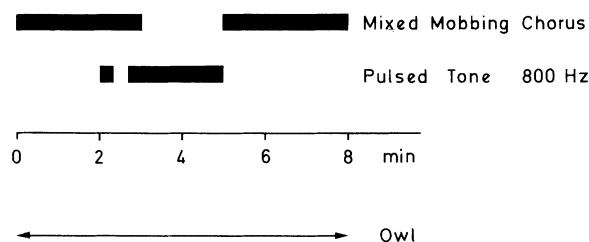

Fig. 1. Stimulus pattern presented to parent great tits 3 m in front of their nest hole. *Upper line:* Mixed species mobbing chorus (see text), with 2 min pause separating continuous train of calls of original tape; *middle line:* 800 Hz pulsed sound (0.8 s at intervals of 1 s) from second track of stimulus tape; *double-head arrow:* presence of live pigmy owl in cage juxtaposed to speaker beaming through the cage

All experimental birds (141 tested with owl, 16 with cat, 72 with predator-free) were feeding *first* broods. Experiments (71 owl, 8 cat, 37 predator-free) were generally spaced so that acoustic stimulation was novel for each pair tested. Except for 1 year, experiments were also separated spatially in consecutive years to minimize familiarization with the set-up. Except for two males, there was no indication of sound learning in previous years. Experiments were run from 8.00 to 18.00 h when it was not raining.

Study areas

All experiments were performed with great tits near Wolfsburg in forested study plots of the Außenstation für Populationsökologie of the 'Vogelwarte Helgoland'. The study plots consisted of Bahrdorf 'Pine Forest', Kampstüh near Hattorf, 'Gutsforst' near Destedt, and the Drömling. The Bahrdorf plot is covered with a mosaic of deciduous (*Fagus silvatica*), mixed, and pine (*Pinus silvestris*) forest. Kampstüh, Destedt, and Drömling are dense, rather humid deciduous forests. Tits nested in boxes of the Schwegler type (Haubersbronn) hung in the trees at a height of 3–4 m. For a fuller description of the study plots see Berndt and Winkel (1967).

Assessment of response to the playback and the predator stimulus

The live predators and the effective sound stimuli both elicited, qualitatively, the same behaviour in both parents if they happened to be out of the nest box. In males, the readiness to attack the owl physically is more pronounced than in females; also only some males exhibited a distraction display close to and directed at the owl (Curio 1980). Brooding females do not leave the nest when hearing a mobbing chorus and were therefore not scored.

Birds approached the stimulus and mobbed it vocally after a certain *latency* that ended when a bird became visible or audible to at least one of the two observers. Latency of response was measured as the time elapsing from the onset of stimulation until a tit was discovered near the stimulus. This interval should reflect the true but unobservable start of responding since the time taken to approach from anywhere in the territory is inconsequential (see p. 133) as compared with the length of the observed latency. One may object that what is taken to be a latency score is in fact due to the next feeding visit of a tit and entirely unconnected with the onset of stimulation. To remove this objection we presented the tits with an experimental situation without the predator + mobbing playback. We ex-

pected the birds to approach their nest later in this case. To test this we set up the bamboo pole used to mount the predator in its cage in the usual way. The tits approached their nest cautiously and finally after a delay visited it to feed. The 'latency' between mounting the pole and the first appearance was found to be 424 ± 563 s (mean $\pm$ SD) in 26 birds of 18 control pairs tested in 1980 in Bahrdorf whereas for 115 experimental birds tested with the live owl + mobbing playback the latency scored was 175 ± 138 s, the difference being highly significant ($P_2 < 0.006$, Mann-Whitney U-test, 2-tailed). It was ascertained that the age of young, a powerful determinant of response intensity (p. 135), did not differ significantly between the two samples ($P_2 \geq 0.09$, Mann-Whitney U-test). Hence, we feel entitled to regard the time from the onset of the test stimulus till the response near the nest as genuinely reflecting latencies, not feeding patterns.

For latency measures to be meaningful one needs to know when great tits are able to perceive the test stimuli, especially the far ranging sound stimuli. As revealed by pilot experiments in September 1982 great tits approached the mixed mobbing chorus from a distance behind the loudspeaker up to 50 m, but not from 70 m. In front of the speaker, the perception possibility improved up to distances of 70 m. These pilot experiments were performed in a Bochum beech forest (Kalwes) resembling the average experimental site, with the loudspeaker 1.5 m above ground and directed horizontally as in our experiments. Since great tits tend to forage within a territory radius of up to about 40 m (Perrins 1979; Smith and Sweatman 1974; personal observation) they can be assumed to hear the playback stimulus from any point in their territory. Even with ambient noise of 40 dB, which is often met in the field, a learnt sine sound wave of 4 kHz would still be heard at a threshold 10 dB lower than this (Klump, personal communication). The average passerine performs well (Dooling 1980).

Considering that neighbouring great tits and other species were attracted to the taped stimulus, it is important to know *how far* it would reach in the forest. Calculations using the formula for total attenuation of sound[1], including excess attenuation in deciduous forest with leaves as tabulated by Marten and Marler (1977, Appendix p. 289. Loudspeaker height 1–2 m), show our taped signals would be transmitted much beyond a great tit's territory radius (40 m).

When oscillating back and forth around the loudspeaker (plus predator), birds attained a *minimal distance* during a trial. This distance was estimated to the nearest 50 cm when the bird was close to the loudspeaker, and to the nearest metre when beyond a distance of ca. 3 m.

Approaching and *vocal mobbing*, called response intensity, RI, was categorized into one of four classes: -0 = silently staying away from the stimulus for the whole of a trial; 0 = approaching the stimulus and staying silent; $+$ = 'churr' phrases (Latimer 1977), rarely other mobbing calls, at a repetition rate of 1–6/min; $++$ = 7–57 'churrs'/min. Calling rate scored was always the peak value (min^{-1}) of a response. For details of the response see Hinde (1952).

The experiments

There were eight experiments with the owl and one with the cat as predator stimulus in the 4 years 1977–1980. Experiments were performed with a varying number of pairs (5–12), which

Table 1. Intra-pair Spearman rank correlations, r, of four dependent behaviour variables used in the multiple regression analysis; mates accurately sexed. *MD* minimum distance from predator. *P* values 2-tailed

Latency of approach LA	Latency of calling LC	Latency of attaining MD	Minimum distance MD
$r = 0.36$	$r = 0.32$	$r = 0.44$	$r = 0.21$
$P \leq 0.036$	$P = 0.069$	$P \leq 0.013$	$P = 0.227$
$n = 35$	$n = 33$	$n = 32$	$n = 36$

differed in year, season and locality. All trials of each experiment were conducted in consecutive hours or days. Experiments differed in the conditioned sound (see Fig. 1): While an artificial 800 Hz sound (88 dB SPL, scale 'Flat', General Radio dB meter, 1 m in front of speaker) was employed in seven (6 owl, 1 cat) of them, an equally novel redwing (*Turdus iliacus*) alarm rattle was used in two other trials; the latter was played back in 1979 with 72 dB in one experiment and with 85 dB (SPL, measured 1 m in front of speaker, scale C, General Radio dB-meter) in the other. The behaviour of the tits was qualitatively the same regardless of the type of sound. Therefore the responses of all eight owl experiments were lumped together in the stepwise multiple regression analysis. The live, caged pigmy owl served as predator stimulus in 72 trials; in five trials (in 1977) the similar Brazilian congener (*G. brasilianum*) was used.

Multiple regression analysis of defence behaviour variables

Five dependent variables were scored for each pair of tits. We assessed to what extent pairs of response scores thus obtained can be regarded as independent within pairs. Only two of the intra-pair correlations of four response measures are significant (Table 1). In view of all r values being low or medium we regard pair mates to act with considerable independence. Accordingly we subjected single bird parameter values, not pairs, to regression analysis. A fifth, ordinal measure, response intensity RI, was scored at only four levels and was therefore not amenable to the regression analysis to follow. This measure will be explored by a contingency table analysis (p. 139ff).

Description of the dependent variables. We selected dependent variables that reflected the risk taken by the great tits. The test stimulus evoked a multi-dimensional mobbing response. Apart from RI, four dependent variables were scored for each bird ($n = 141$) of a pair if possible:
(1) *Latency of approach (LA)* towards the compound stimulus denotes the time from the onset of the mobbing playback until a great tit parent was spotted in the canopy surrounding the nest and our set-up. Since after arrival tits never departed again during an ongoing trial, a short latency means a longer exposure to danger, and, hence, a higher risk, all other things being equal. A number of birds came only after stimulation had ceased but they demonstrated by their calling that they had perceived the danger earlier. Also a few birds (ca. 5%) arrived after only 0–10 s, i.e. far ahead of the average bird (needing 175 s [$n = 115$]). Assuming that great tits fly about 12 m/s, a conservative estimate (see Herzog 1968), and assuming a territory radius of up to about 40 m around the nest (Perrins 1979), a bird would need no more than 3–4 s to arrive at the stimulus from even the most distant point of its territory (see also Smith and Sweatman 1974) when it hears the onset of the mobbing tape. Hence, tits hesitate to approach the speaker despite perceiving the broadcast and hide themselves in the canopy.

---

1 Maximum distance d is obtained by numerically solving the equation: source intensity-hearing threshold $= 20 \log d + $ excess attenuation $d/100$ dB; for d, when source intensity is measured 1 m from loudspeaker

(2) *Latency of calling (LC)* is the time from the start of the tape until the first mobbing call, mostly a '*churr*', less commonly '*tsi huit*', or some other vocalization which in the male may also be heard in song. These latter calls were only uttered 1–3 times until trains of '*churrs*' took over for the rest of the trial. In the majority of cases vocalizing followed approach, in only two birds (4.3%) the reverse occurred. Accordingly, when the calling of a bird that we had not spotted before started, LA was set equal LC. In such cases we had the impression that the distance of the mobber from the stimulus was about the same as for a spotted tit which was still silent. This could mean that the tit had been silently observing the scene from cover so that overall LA had been somewhat overestimated (see p. 135). The onset of calling was thought to be less susceptible to observation error. This idea, however, receives no support from individual variation of both scores: mean $LA \pm SD = 175 \pm 138$ s ($n = 115$) vs mean $LC \pm SD = 247 \pm 201$ s ($n = 109$).

(3) *Minimum distance (MD)* is the shortest distance between the birds and the test stimulus. When the existing vegetation did not provide cover up to about 0.1 m from the stimulus, we placed branches there. MD is thought to reflect most accurately the risk taken.

(4) *Latency of attaining minimum distance (see 3) (LMD)* was measured from the onset of the stimulus.

Description of the independent variables. To study the impact of factors potentially determining risk, as measured by the above-mentioned four dependent variables, the following independent variables were used:

(1) *Temperature* was measured to the nearest °C and was included because of consideration of the energy budget.

(2) *Wetness vs dryness* tests the dichotomized influence of plumage conditions, the prediction being that a wet plumage due to dew or rain would cause birds to behave less risk-prone. We did not do any trials in the rain, but we did not avoid trials just after the rain.

(3) *Habitat* was classified as *broad-leaved* or *coniferous forest* because of the possible influence on parental effort via reproductive value. The benefit/cost ratio of a current brood is higher for a single-brooded bird not embarking on a second brood in the same season. This is more likely in broad-leaved forests where second broods are distinctly rarer (see Curio and Regelmann 1982).

(4) *Cover* provided by the canopy surrounding the site of presentation was scored by its distance to the nearest half metre. Our prediction was that birds would take more risk when cover was close than when it was distant.

(5) *Season:* Original dates were transformed by starting with the earliest date (19 May = day 1) with all subsequent dates derived by adding the number of days elapsed since. From the day thus obtained the mean of all transformed dates was subtracted and the number of days that the young were still expected to stay in the nest was added (based on standard nestling period of 20 d). This procedure is thought to express the prospects for a second brood, the prediction being that late birds would put more effort into their current nesting attempt; early breeding birds would enjoy a higher residual reproductive value because of producing more second broods and thus should invest less (Curio and Regelmann 1982).

(6) *Brood size*, or number of young, was recorded after trials. If parents gear their efforts to expected future benefits, then a large brood should be defended more (Emlen 1970; Robertson and Biermann 1979).

(7) *Age of young* (according to the criteria by Winkel 1970) and brood size were recorded at the same time. Runts up to

several days younger than the rest of the brood were not considered.

(8) '*Brood value*' is a measurement computed from the number, age, and mortality of the nestlings plus parents (see Curio and Regelmann 1982). The measurement is thought to express dynamically the value of a brood as opposed to measures mentioned in (6) and (7).

(9) *Sex* of the responding bird.

(10) *Presence vs absence of a mate prior and up to LA* (see dependent variable 1). The mate might act as a numerical divider of risk (a), possibly also as an insurance against being cheated (b) (Chase 1980).

(11) *Presence vs absence of mate prior and up to LC* (see dependent variable 2). Rationale as under (10).

(12) *Number of birds (excluding mate) prior and up to LA* (see dependent variable 1). Rationale as under 10 (a).

(13) *Number of birds (excluding mate) prior and up to LMD* (see dependent variable 4). Rationale as under 10 (a).

(14) *Number of birds (excluding mate) present, during and after trial* ('after-response') should reflect that part of the surrounding avifauna willing to take a risk in harrassing a predator. Upon termination of a trial, none, one or several individuals used to come and mob. The measurement has the virtue of being constant during a trial.

(15) *Year,* varying over four categories 1977–1980, was considered to be important because of, e.g., annual fluctuations of laying and harshness of climate. These factors could, for example, give rise to constraints of defence. The influence of the year will only be examined after filtering out irrelevant independent variables.

A further independent variable, the role of the mate, was conceived of in the course of the analysis (see p. 139).

Results

The multidimensionality of the response

Before considering what factors influence brood defence, we will clarify whether responses to the owl and the mobbing chorus are multidimensional, i.e. whether any of the dependent variables can be replaced by any other of the dependent variables. To this end, Spearman rank correlations were computed between dependent variables (Table 2). From an inspection of the correlation coefficients it follows that most relationships are so weak that mobbing cannot be considered unitary. Hence, we will keep all the response variables in the analyses that follow.

The relatively high positive correlations between the variables LA and LC, and between LA and LMD led us to examine further their meaning. For example, can LA be taken as a substitute for LC or LMD? Since in the sequence of events birds take less time to show up than to investigate the owl closely, i.e. $LA \leq LMD$, and since in most cases they show themselves before calling, i.e. $LA \leq LC$, the differences $LMD - LA$ and $LC - LA$ were regressed on LA producing the following regression equations:

Table 2. Spearman rank correlations r between dependent variables; response intensity as measured by approach and mobbing vocally $= 0$, $+$, $++$ (see p. 133). *Number of individuals*, P values 2-tailed

	Latency of calling		Latency of attaining MD		Minimum distance		Response intensity calls/min	
Latency of approach (s)	$r = 0.78$ $P \leqq 0.001$	*100*	$r = 0.60$ $P \leqq 0.001$	*93*	$r = 0.12$ $P = 0.22$	*108*	$r = -0.43$ $P \leqq 0.001$	*97*
Latency of calling (s)			$r = 0.46$ $P \leqq 0.001$	*90*	$r = 0.14$ $P = 0.17$	*102*	$r = -0.47$ $P \leqq 0.001$	*94*
Latency of attaining MD (s)					$r = -0.09$ $P = 0.38$	*97*	$r = 0.04$ $P = 0.75$	*87*
Minimum distance (m)							$r = -0.31$ $P \leqq 0.001$	*113*

$$LC - LA = 0.02 \cdot LA + 79.5$$
$$(P_b = 0.88; n = 100),$$

and

$$LMD - LA = -0.28 \cdot LA + 159.6$$
$$(P_b \leqq 0.003; n = 93),$$

where P_b give 2-tailed significance of b values. This means (1) Upon approach the birds start calling with a delay of on average 80 s and (2) The later a bird approaches, the earlier it attains its minimum distance (MD) thereafter. To explain the latter negative relation between $LMD - LA$ and LA given in the second of the regression equations mentioned above, two hypotheses were formulated:

(1) While approaching the owl when still under protection of cover, the tits observe the owl and the mobbing party and assess their risk of joining the party. Tits that observe for longer get a better estimate of their risk and can therefore afford to attain their MD earlier after joining the mobbing party.

(2) When a tit joins the mobbing party the number of birds in the party increases. Thus tits that approach later can afford to attain their MD earlier because of less risk or other risk-diminishing effects due to group numbers.

We found no significant Spearman rank correlation between $LMD - LA$ and the number of birds prior and up to LA (variable 12) ($r_s = -0.11$, $P_2 = 0.3$, $n = 92$). Partialling out the latter variable (12) leaves the correlation between $LMD - LA$ and LA unaffected ($r_s = -0.33$, $P_2 < 0.003$, $n = 92$). Therefore hypothesis (2) can be rejected: Having observed the danger situation for longer, tits can afford to attain their MD earlier.

Despite the close connection between LA and LC, we retained both response variables in the analysis

that follows. They turned out to be differentially sensitive to a number of independent variables including the year of experimentation.

Stepwise multiple regression analysis (= SMRA)

As a first step towards an evaluation of the factors that influence the multidimensional mobbing response, apart from the stimulus applied, a stepwise multiple linear regression analysis (= SMRA) (Sokal and Rohlf 1981) was carried out. The results of the computer analysis using SPSS routine REGRESSION (Beutel et al. 1980) are given in Table 3, from which MD was left out because of no influence from any of the independent variables tested. Based on a less complete (cover [4]) data base, the variable Cover turned out to have no significant influence.

Contrary to our expectations (see p. 134), only age of young (7), not brood size (6) or brood value (8), has an incremental influence as predicted, but it does so only on LA.

We regarded the variable season (5) as an indication of the tits' future chances to start a second brood. The argument was that tits with late broods, i.e. having high values of season (5), have only a small chance to start a second brood and should therefore invest more into their current first brood. By contrast, we found that the later tits bred, the more reluctant they were to attain their shortest distance to the danger (LMD, Table 3). However, this finding of a positive relation between season (5) and LMD may be caused by differences between years not considered in this preliminary analysis (see pp. 138, 141).

Since tits living in coniferous forests are more likely to start a second brood (Kluijver 1951; van

Table 3. Stepwise multiple linear regression analysis with independent variables (columns, numbering see text) regressed upon dependent variables of scores (rows) in responses to owl + mobbing chorus playback. β values are standard partial regression coefficients and R values are multiple correlation coefficients (Sokal and Rohlf 1981); n number of individuals; P values 2-tailed. As the variables temperature (1), brood size (6), and brood value (8, see text) did not enter any of the three regression equations at any level of significance ($P<0.05$) they are omitted from the above table. No entries denote non-significant β

Dependent variables	Independent variables										
	Wet (=1) vs dry (=0)	Habitat broad-leaved (=0) coniferous (=1)	Season	Age of young	Sex ♂=0 ♀=1	Presence (=1) vs absence (=0) of mate prior and up to LA	Presence (=1) vs absence (=0) of mate prior and up to LC	Number of birds prior and up to LA	Number of birds prior and up to LMD	Number of birds during and after trial	
	(2)	(3)	(5)	(7)	(9)	(10)	(11)	(12)	(13)	(14)	R
Latency of approach LA $n=81$	$\beta=-0.31$ $P\leq 0.001$	$\beta=-0.19$ $P\leq 0.02$		$\beta=-0.33$ $P\leq 0.001$		$\beta=0.18$ $P\leq 0.022$	[a]	$\beta=0.66$ $P\leq 0.001$	[a]	$\beta=-0.19$ $P\leq 0.045$	0.75
Latency of calling LC $n=78$	$\beta=-0.24$ $P\leq 0.01$	$\beta=-0.30$ $P\leq 0.002$			$\beta=0.22$ $P\leq 0.045$		$\beta=0.32$ $P\leq 0.003$	$\beta=0.24$ $P\leq 0.012$	[a]		0.65
Latency of attaining MD LMD $n=70$		$\beta=0.29$ $P\leq 0.003$						$\beta=0.36$ $P\leq 0.016$	$\beta=0.36$ $P\leq 0.021$	$\beta=-0.26$ $P\leq 0.03$	0.67

[a] Variables were not used in the respective computer analysis since β were meaningless because of sequence of events

Balen 1973) we had expected they would invest less into their first broods than tits living in broad-leaved forests (Curio and Regelmann 1982). However, we actually found that tits living in coniferous forest take more risk as measured by LA and LC (Table 3).

That ♂ tits risk more in brood defence than ♀ tits (Curio 1980) is corroborated by one result in Table 3. Male tits start calling earlier.

Our prediction that in wet weather tits would respond more cautiously is not borne out. Instead they approach and call earlier in wet weather. This, together with the finding that a low ambient temperature facilitates responding (p. 137), leads one to consider heat load of a working bird as a constraint. In some of the experiments ambient temperature approached the range of thermo-neutrality, which in great tits lies at about 32–35° C (Rautenberg, personal communication). Japanese quail (*Coturnix c. japonica*) suffer from excessive heat load during enforced exercise (Nomoto et al. 1983), comparable in effect to the work load of parent tits feeding young. A wet plumage due to its cooling effect probably partially alleviates heat load.

The positive relations between the independent variables 10, 11, 12, 13 (for explanations see Table 3) and the latency measures LA, LC and LMD (Table 3) can hardly be seen to reflect adaptedness of behaviour. It is more likely that these positive relations are due to a time effect of measurement: The later a bird approaches, starts calling, or attains its MD the more likely it is that its mate is present and the number of all other birds attending has increased. This interpretation is supported by a negative relation between LA and LMD and the independent variable (14) which is *not dependent* on time. Variable (14) reflects the number of potential mobbers at a place; it most likely represents a measure of the number of birds living within earshot of a particular tit's nest. Thus the negative relation of variable (14) with LA and LMD may indicate that the tits make use of some risk-diminishing effects due to group numbers.

What fraction of the total variance of brood defence is explained? In Table 3 multiple correlation coefficients R (Sokal and Rohlf 1981) are given. R values were computed when all independent variables with significant β-values had entered the regression equation. Since $R^2 \leq 0.57$ for all three dependent variables (LA, LC, LMD), a large fraction of the variance of the dependent variables is left unexplained, although a large number of independent variables have been examined.

One can now ask whether the independent variables are uncorrelated immediate causes of the de-

Table 4. Spearman rank correlations r between latency measures (columns) of responses to owl + mobbing chorus playback and independent variables (rows, with $P<0.05$ for at least one latency measure): numbering same as in text; *number of individuals*, P values 2-tailed

		Latency of approach LA		Latency of calling LC		Latency of attaining MD LMD	
(1)	Temperature	$r = 0.27$ $P \leq 0.004$	*114*	$r = 0.26$ $P \leq 0.006$	*108*	$r = 0.09$ $P = 0.4$	*99*
(3)	Habitat broad-leaved (=0), coniferous (=1)	$r = -0.20$ $P \leq 0.029$	*115*	$r = -0.25$ $P \leq 0.011$	*109*	$r = -0.19$ $P = 0.062$	*100*
(4)	Cover	$r = -0.14$ $P = 0.24$	*76*	$r = -0.16$ $P = 0.17$	*74*	$r = -0.29$ $P \leq 0.014$	*72*
(5)	Season	$r = 0.19$ $P \leq 0.041$	*115*	$r = 0.17$ $P = 0.074$	*109*	$r = 0.28$ $P \leq 0.005$	*100*
(6)	Brood size	$r = 0.19$ $P = 0.051$	*108*	$r = 0.24$ $P \leq 0.014$	*103*	$r = 0.15$ $P = 0.14$	*95*
(7)	Age of young	$r = -0.24$ $P \leq 0.009$	*115*	$r = -0.12$ $P = 0.22$	*109*	$r = -0.16$ $P = 0.12$	*100*
(8)	Brood value	$r = 0.11$ $P = 0.24$	*108*	$r = 0.23$ $P \leq 0.02$	*103*	$r = 0.14$ $P = 0.16$	*95*
(9)	Sex ♂=0; ♀=1	$r = 0.26$ $P \leq 0.015$	*88*	$r = 0.34$ $P \leq 0.002$	*85*	$r = 0.17$ $P = 0.135$	*82*
(10)	Presence (=1), vs absence (=0) of mate prior and up to LA	$r = 0.26$ $P \leq 0.007$	*107*	$r = 0.31$ $P \leq 0.002$	*98*	$r = 0.21$ $P \leq 0.046$	*90*
(11)	Presence (=1), vs absence (=0) of mate prior and up to LC	[a]		$r = 0.37$ $P \leq 0.001$	*102*	$r = 0.23$ $P \leq 0.03$	*89*
(12)	Number of birds prior and up to LA	$r = 0.52$ $P \leq 0.001$	*113*	$r = 0.41$ $P \leq 0.001$	*105*	$r = 0.40$ $P \leq 0.001$	*93*
(13)	Number of birds prior and up to LMD	[a]		[a]		$r = 0.39$ $P \leq 0.001$	*95*

[a] r meaningless because of sequence of events

pendent variables or whether they are correlated among each other. In the orthogonal case, i.e. when the n independent variables in a regression analysis are uncorrelated the following equation holds

$$R^2 = \sum_{i=1}^{n} \beta_i^2.$$

Since the above equation does not hold in our case with n being the number of independent variables with a significant β (see Table 3), we conclude that at least some of the independent variables are correlated. Because of the large number of variables and the lack of models describing relations between these and the independent variables, we felt unable to use path analysis (Sokal and Rohlf 1981) as a tool for further analysis.

Correlation analysis

To examine the results of the foregoing regression analysis and to obtain information based on greater numbers of individuals, Spearman rank correlations were computed between the variables LA, LC, LMD and MD and all of the independent ones except for variable (15) (Table 4). The results support and extend those of the SMRA. It is interesting to find brood size (6) to be positively correlated with LC; the more young parent tits have, the later they start calling. A similar effect is also indicated by the two other latency measures though not significantly. This finding, although not indicated by the regression analysis, runs totally *counter* to our prediction.

Ambient temperature ranged from 13° C to 32° C during presentations. High temperature constrains rather than facilitates responding as expressed by two of the three latency measures. The same explanation applies to the facilitatory effect of a wet plumage (p. 136), in that a bird risks less when suffering from an excess of heat due to the strain of feeding, exacerbated by the (expected) additional heat load of mobbing. High temperatures

up to 28° C lead a female to leave her eggs for longer and during incubation spells to stay less on the eggs (Kluijver 1950). Both aspects could be accommodated by assuming that the female dissipates excess heat more easily when outside the nest hole.

Annual variation of nest defence

The reluctance of the tits to respond to the playback stimulus in 1980 led us to ask whether the responses to the test stimulus differed between the years. The initial SMRA had shown brood defence to be influenced by many factors. Since these tend to vary between years it was ascertained that annual differences of responses were not due to the corresponding differences of those independent variables. After converting the variable year into dummy variables we tested whether their inclusion into multiple linear regression analyses for each dependent variable led to an increase of R, i.e. of the portion of variance of the dependent variables explained (multivariate F-test, Gaensslen and Schuboe 1976). It turned out that only the dependent variables LA and LC were affected differently in different years ($P_2 < 0.05$, $P_2 < 0.01$, respectively). Thus the questions arise:

(1) Which years are responsible for the differences? A more detailed analysis revealed that tits approached the danger later in 1980 than in 1977–1979 ($P_2 < 0.01$), and they started calling later in 1979 ($P_2 < 0.004$).

(2) To answer the question of what might be candidate factors causing differences between years, we entertained the idea that nestling mortality differed between years. Comparing nestling mortality between years showed it peaked at 0.0405/day in 1978 whereas it was extremely low in 1979 amounting to a mere 0.005/day ($P_2 < 0.006$). The benefit/cost ratio (present number of young fledging/Residual Reproductive Value, see Curio and Regelmann 1982) should have induced tits to invest more parental effort in 1979 since the prospects of fledging were extremely good. Only their earlier approach in 1979 as compared with 1980 is consonant with such a view.

A further factor of potential influence is annual variation of hatching time. Therefore, we computed the mean annual hatching dates and found that they differed between years ($P_2 < 0.001$, $n = 269$, Kruskal-Wallis H-test), since hatching was later in 1979 than in all other years ($P_2 < 0.001$, $n = 269$, Mann-Whitney U-test). However, mean hatching dates must also be regarded to differ significantly among 1977, 1978 and 1980 ($P_2 < 0.001$, $n = 204$, Kruskal-Wallis H-test).

A late season means a low Residual Reproductive Value because of the reduced prospects for a second brood in the same season. Hence the benefit/cost ratio should have been especially favourable in 1979 predicting a high parental effort. However, the expectation of a lower incidence of second broods in 1979 was fulfilled in only one area (Destedt 4% of the successful first brood birds, Sprötge, personal communication), not in the two others (Kampstüh 24%, Bahrdorf 48%, Winkel, personal communication). The type of habitat appeared to be of greater importance.

Since in 1980 tits proved unusually reluctant to approach the scene but started nesting as usual, we looked for another factor to account for the long LA. There had been night frosts during the laying/incubation period in 1980 so that the foliage of several trees (beech, oak) had turned black. Eggs did not hatch and a female died on the nest. The average temperature in the 1st 10 days of May, though, was only the second lowest of all four years (Deutscher Wetterdienst Braunschweig-Völkenrode, Winkel, personal communication). May 1980 as a whole proved to be the coldest May of all four years (av. temp. 11.2° C; range 12.1–13.1° C for 1977–1979). Hence, the delay in approaching in 1980 may have been the expression of a constraint due to an energetic strain of the adult tits rather than an adaptive response in terms of life-history.

(3) To answer the question whether annual differences would affect the conclusions from the initial regression and correlation analyses, we computed new correlation matrices like the one in Table 4 for each year separately and ran a new SMRA for 1979 solely, the year with the broadest data base. Conclusions have to be revised in three respects:

(a) In the SMRA for 1979 there is now a negative relation of distance from cover (4) with LMD (contrasting Table 3, where (4) dit not enter, p. 136), and, for the first time, a positive relation of cover (4) with MD ($P_2 < 0.002$ and $P_2 < 0.035$, respectively). In the new correlation matrices trends were similar although the correlations were in most cases not significant ($P_2 > 0.05$).

(b) In 11 out of 16 cases (4 dependent variables· 4 years) season (5) was now negatively correlated with one or another of the response variables LA, LC, LMD, and MD. Although in most cases these correlations were not significant ($P_2 > 0.05$) we feel that this result lends support to our prediction that tits that have a *lower* chance to start a second brood should invest *more* into their first brood (see p. 134).

(c) Finally, we found negative correlations between brood size (6) and the response variables in 10 out of 16 cases but none of the 16 correlations was significant ($P_2 > 0.05$). This result runs counter to those in Table 4 where we found one significant positive correlation, i.e. of brood size (6) with LC. Our prediction that parent tits with more young should invest more into brood defence was not borne out by any of these analyses.

The rôle of the mate

Mates of a pair are expected to cooperate in caring for the young. We asked whether presence vs absence of the mate has an influence on the responses to the test stimulus. Since latency measures LA, LC, LMD and variables (10), (11) (see Table 4) could not answer the question because of time effects of measurement (p. 136), we concentrated on MD. As a new variable, we examined whether the mate was present when an individual tit attained its MD. From Table 5 it can be seen that, first, in the presence of its mate a ♂ approaches more closely than a ♀ ($P_2 < 0.005$, $n = 53$, Mann-Whitney U-test), thus corroborating an earlier finding (Curio 1980). Second, ♂ dare to approach the enemy more closely in the presence of the ♀ than when alone ($P_2 < 0.02$, $n = 39$, Mann-Whitney U-test).

At first sight the result could mean that a ♂ is encouraged by the presence of its mate to approach the owl more closely because it strives to protect its mate by drawing the owl's attention to itself or for other reasons. Alternatively, mates of a pair could share common factors. There may be pairs whose mates are willing to mob only weakly causing the ♀ to stay away in cover or approach later and the ♂ to keep further away from the owl. At the other extreme there may be pairs that are willing to mob more intensely with the ♀ approaching earlier and the ♂ approaching the owl more closely. To examine the latter idea, we ran a multiple linear regression analysis based on all ♂, with the dependent variable MD and the independent variables 5, 6, 7, 13, 14 (see p. 134 seq.) and a new independent variable denoting presence vs absence of the mate prior and up to LMD. Only the latter variable had a significant impact on the male's MD ($P_2 < 0.003$). Thus, the above objection of between pair variation of responsivity can be rejected.

Is the rôle of the ♀ mate unique or could it be played by any bird approaching danger? To examine this question we computed the mean MD for all ♂ whose mate had appeared before any other bird from the neighbourhood had arrived.

Table 5. Minimum distance MD (m) from owl (mean±SD) of parent tits as a function of the presence of the mate

Sex	Mate	
	Present	Absent
♂	1.0±0.8 n=24	2.3±2.1 n=15
♀	2.1±1.5 n=29	2.0±2.0 n=4

With this value we compared the mean MD when another bird but not the ♀ was present in the moment of attaining MD. The means were 0.9±1.0 m and 2.7±2.6 m (mean±SD), respectively. The difference of almost 2 m is significant ($P_1 < 0.05$, n_1, $n_2 = 11, 8$, Mann-Whitney U-test). This again demonstrates that it is uniquely the presence of the ♀ which makes the ♂ attain a smaller MD.

Mobbing intensity as a function of properties of the brood: a re-examination

Parent tits were shown to take more risk with increasing age of the young (7), as we expected, but were unresponsive to the number of young (6), a measure most directly connected with fitness. Since the latter finding runs counter to prevailing theory (e.g. Robertson and Biermann 1979) we decided to reexamine the discrepancy by using data of response intensity (RI) as measured on an ordinal scale (−0, 0, +, ++, p. 133). It is only during calling (+, ++) that some parents indulge in vigorous attacks on the pigmy owl, and that all parents completely refrain from feeding. Attending a trial (0, +, ++) and even more so homing in on the owl poses more risk to the tits than staying away.

Nestling age. To examine whether nestling age (7) and sex (9) affect RI a three-way contingency analysis (G-test) was performed on the conditioning trial (Table 6a); both the test for learning to mob the artificial predator sound and conditioning in a 'predator-free' paradigm yielded similar results (Tables unpublished). RI is a function of one independent factor, namely sex or age, regardless of the level of the other. An inspection of the figures shows males to respond more strongly than females, thus confirming an earlier finding (Curio 1980).

The observed increase of RI with nestling age is most pronounced after day 12 when −0 responses have disappeared completely. The ten-

Table 6. Mobbing intensity RI (scores see p. 133) as a function of (a) nestling age ($n = 362$ parents) and (b) brood size ($n = 292$ parents), in addition to sex of parent. Owl + tape stimulus. Three-way contingency analysis (G-test) after Sokal and Rohlf (1981)

H_0	G	df	P_2
a No 3-factor interaction of RI, age, sex	1.19	6	0.98
Independence of age, sex conditional on level of RI	0.74	2	0.69
Independence of RI, sex conditional on level of age	21.84	3	0.00007
Independence of RI, age conditional on level of sex	24.09	6	0.0005
b No 3-factor interaction of RI, brood, sex	2.47	6	0.87
Independence of brood, sex conditional on level of RI	0.63	2	0.73
Independence of RI, sex conditional on level of brood	16.39	3	0.0009
Independence of RI, brood conditional on level of sex	12.07	6	0.06

dency to emit mobbing calls increases significantly after 12 days of age; the increase of calling from 75.6% ($n = 123$) to 98.3% of the responses ($n = 58$; $\chi^2 = 14.27$; $df = 1$, $P_2 = 10^{-4}$) happens at the expense of both the non-vocal -0 and 0 responses. The complete disappearance of -0 responses after the age of 12 days proves that the birds are *capable* of detecting the visual/acoustic stimulus at their nest; staying away is a genuine *decision of predator avoidance*, not a consequence of inadequate stimulation. Unexpectedly, the proportion of the strongest, the $++$ among the vocal responses decreases after the age of 12 days from 41.9% ($n = 93$) to 22.8% ($\chi^2 = 5.71$, $df = 1$, $P_2 = 0.017$).

Brood size. RI is marginally related to brood size (6) but significantly to the sex of the parent (9) (Table 6b). Again, ♂ respond more strongly, regardless of brood size (non-significant interaction).

Contrary to theoretical expectation, but in line with our previous findings, RI *decreases* over part of the range with *increasing* brood size; the relative proportion of stay away responses (-0) increases, both relative to the silent responses (0) ($\chi^2 = 6.053$, $df = 1$, $P_2 = 0.014$, brood sizes 1–8, 9–12) and relative to the rest of the responses ($\chi^2 = 8.054$, $df = 2$, $P_2 = 0.018$). This means parent birds tend to be more active in *avoiding* the risk of showing up near the predator the *more* young they care for.

The decrease of RI after day 12, as measured by the vocal responses, and with growing number of young, suggests a constraint to operate since the relationship runs counter to the prediction. A potential constraint may be physical fatigue of parent birds. Gibb (1955) found that parent great tits of large broods increase the feeding rate in the first half of the nesting period, that but they slackened off in the second half. This did not happen in small broods. Moreover, in the afternoon the

pairs with large broods did not attain the second peak of feeding activity typical of other pairs. If physical fatigue were the reason for the decrease of RI with brood size, the effect should be aggravated in older broods.

The prediction that RI should become smaller with age only in large broods (9–12) was tested in two ways: (a) In large broods with old (7–21 days) nestlings the relative proportion of silent -0, 0 responses becomes greater, though not significantly, than in younger ones (36.8%, $n = 19$, vs 20%, $n = 15$). (b) The incidence of silent responses in parents with older young (13–21 days) increases with brood size from 0% ($n = 20$, 1–8 young) to 57% ($n = 7$, 9–12 young) ($P_2 < 0.02$, Fisher exact test). Hence, a large brood size seems to prevent parent birds from increasing RI with nestling age as would be predicted from knowledge of the dependency of RI on age alone (see Table 6).

How do parents behave when under less strain because of feeding younger nestlings? An inspection of the RI scores from parents with young nestlings (1–8 days old) does not show any correlation with brood size. This seems to rule out the possibility that parent birds are constrained under *all* circumstances to raise RI with brood size.

Annual differences of response strength RI. As with other response variables before (p. 138 seq.), we examined whether combining the data from all years had obscured relationships between RI and brood size (6). We neither found a dependence of RI on brood size in predator-associated conditioning nor in the subsequent test for 1977, 1978 and 1979; nor was there an effect of any particular year ($P_2 = 0.1$, conditioning; $P_2 = 0.7$, test). An effect of the latter sort was, however, present in 'predator-free' experiments. While three years (1977, 1978 and 1980) did not differ in RI from parents

Table 7. Mobbing intensity RI (p. 133) as a function of nestling age and year, as recorded during 'predator-free' conditioning (mobbing chorus + artificial sound playback). Sexes pooled. χ^2-test for 3 years; G-test for 2 years; all ages

	Nestling age (days)	RI			
		-0	0	$+$	$++$
1977	13–21[a]	0	1	10	1
1978	1–12	0	0	14	2
	13–21[a]	0	0	2	2
1980	1–12	4	7	1	0
	13–21[a]	1	3	8	6

[a] $\chi^2 = 6.406$; $df = 6$; $P_2 = 0.4$

H_0 for 1978, 1980	G	df	P_2
No 3-factor interaction of RI, age, year	4.83	3	0.184
Independence of age, year conditional on level of RI	12.35	1	0.0004
Independence of RI, year conditional on level of age	19.78	3	0.0002
Independence of RI, age conditional on level of year	11.76	3	0.0082

with broods aged 13–21 days (Table 7, $P_2 = 0.4$) there is clearly a difference between responses of parents from 1978 and 1980 ($P_2 = 0.0002$, G-test). This effect must be independent from the different nestling age composition since there is an impressive variation *within* an age class (1–12 days). The difference between 1978 and 1980 lies in the strange lack of -0 and 0 responses in young brood birds in 1978 while in 1980, RI increases with age as expected ($P_2 < 0.002$, Fisher exact test). Readiness to respond was, hence, greater in 1978, corroborating the finding that tits approached danger later (LA) in 1980 (p. 138).

Discussion

General

A large number of factors has been found to be correlated with the intensity of brood defence behaviour. Figure 2 provides an overview of these relationships under the assumption that the independent, contextual variables are causal factors, either proximately or ultimately. The putatively causal effects vary in strength as mirrored, for example, by the magnitude of the standard regression coefficients β (see also Tables 3, 4). Since they do not scale, the effects of the year cannot be categorized as incremental ($+$) or decremental ($-$).

We envisage response strength equivalent to magnitude of risk taken because the correlation

found between the response variables are in the direction (Table 2) predicted by us a priori. An exception is MD, which is neither correlated with any latency measure in a way we expected (short latencies – short MD) nor in any other meaningful way, except for its relation with RI (Table 2; see Regelmann et al., in preparation).

Different response variables determined by different contextual factors

Whereas 4 out of 5 dependent behaviour measures are affected by a large set of factors (Fig. 2, top), the fifth, MD of the ♂, is strongly ($P_2 < 0.003$) and uniquely influenced by the presence of the ♀ mate prior to the attainment of MD (Fig. 2 bottom): When the ♀ is present, the ♂ homes in on the owl twice as close as when he is alone.

Evidence is accumulating that the major function of avian mobbing is moving on the predator (e.g. Bildstein 1982; Shedd 1982; Regelmann et al., in preparation), thus benefitting the mobber(s) and the brood. As shown by the fact that the ♀ elicits a closer approach of the ♂ towards the predator there must be an auxilary beneficial consequence, at least for the ♂. In this way he incurs a still higher risk than he would do otherwise (Curio 1983a; Regelmann et al., in preparation). Any simple Selfish Herd Effect (Hamilton 1971) can be safely ruled out because it rests on the premise that the predator invariably selects the closest victim. We conjecture that the male's closer approach
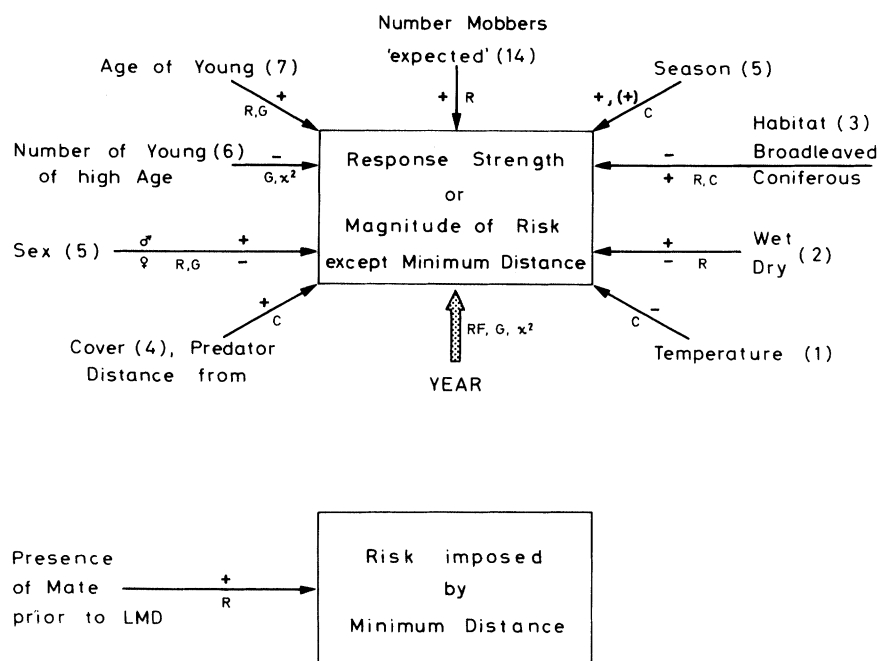
Age of Young (7)

Number Mobbers 'expected' (14)

Season (5)

Number of Young (6) of high Age

Sex (5)

Cover (4), Predator Distance from

+ R,G

+ R

+, (+) C

Response Strength

or

Magnitude of Risk

except Minimum Distance

– G, x²

♂ + ♀ – R,G

+ C

RF, G, x²

YEAR

Habitat (3)
Broadleaved –
+ R,C Coniferous

Wet +
– R Dry (2)

– C

Temperature (1)

Presence
of Mate
prior to LMD

+ R

Risk imposed

by

Minimum Distance

Fig. 2. Synopsis of the effects of independent variables on the risk taken by parent great tits as measured by three latency measures (LA, LC, LMD), the intensity of mobbing (RI) (top) and by the minimum distance (MD) attained while approaching the predator (owl, cat). Of 16 independent variables tested (numbers 1–15 see p. 134 seq.; 'Presence of Mate ...' see p. 139) only those with significant effects are included ($P_2 < 0.05$): Multiple regression analysis R, correlation analysis C, three-way contingency analysis G, R via a dummy variable (year) subjected to F-Test RF. Positive influence ($+$) denotes increase of risk taken, a negative ($-$) denotes decrease of risk with growing magnitude (or change) of independent variable. Single year effects by season (5) regarded as more realistic than correlations across all 4 years. Further explanations see text

protects the ♀ staying behind the ♂, or the ♂ risks more in order to show off prowess to the ♀ and so keep her bonded for future broods as great tits tend to pair for life (Winkel and Winkel 1981).

The deviant causal and functional relationships of MD may explain why all latency measures including LMD are so weakly correlated with MD (Table 2). It should be noted, however, that none of the correlations among the dimensions of brood defence is particularly strong (Table 2). Hence, the latter may be subjected to varying demands, provided the response as a whole is adapted (but see below). The sexual difference in MD shows up only in the presence of the mate, otherwise there is perhaps no difference (Table 5). This explains why sex is no determinant of MD in Fig. 2 since the data from all trials have been combined regardless of the presence of the mate. The small sample size of ♀ that respond in the absence of the ♂ (Table 5) precludes any firm conclusion as to whether the ♀ would differ in her behaviour from that of the male.

What fraction of the response variance can be explained?

Despite the consideration of 16 contextual variables the fraction of the total variance explained for the three latency measures subjected to SMRA is less than 57% (Table 3, $R^2 \leq 0.57$). Being impressed by the enormous variation of the many facets of the response, recorded and unrecorded,

among the trials, we cannot escape the feeling that it is *individual variation* that makes up for response unpredictability. RI, as measured by the rate of calling, has been found to be typical and persistent in time for the individual pied flycatcher (*Ficedula hypoleuca*) (Curio 1975). Similarly, in the great tit intra-individual correlations of response variables in two similar stimulus conditions a day apart are all positive though seldom significant (unpublished data). The number of independent contextual factors is in reality smaller than indicated (p. 137). For example, temperature (1) and wetness of the forest (2) most probably become one common denominator. It can be seen as facilitating dissipation of heat accumulated by feeding the nestlings (see Nomoto et al. 1983). This simpler explanation runs counter to our predictions, generated for both effects separately, which can be regarded falsified even if one does not accept the common factor explanation just proposed. By contrast, age and number of young, and sex act additively on RI.

Constraints and restraints

Constraints determine what can evolve. Usually viewed as proximate factors constraints that become effective in the future can act as ultimate factors and are called here *restraints*. This thinking is in accord with recent developments of life history theory (review Stearns 1976). Constraints are due to at least three different reasons:

(1) The rate of responding has an upper limit because *time* is a constraint on a further increase

of the rate ('efferent saturation' Curio 1975; 'ceiling effect'). 'Churr' calls by great tits seldom exceed a rate of 10–20 calls/min but 54 calls/min are possible (Klump, personal communication). Therefore, the calling rate is probably not constrained by time. This is supported by the fact that the average RI increases with the age of the nestlings although the strongest responses (+ +) decrease in number.

(2) *Physiological capability* constrains, e.g. MD to ca. 1 m, because of manoeuvrability and flight speed. It is only during mock attacks on the owl that the tit attains a MD of about 0.1–0.2 m, that is when its momentum of flight permits it to forestall a potential attack. Likewise, the need for effective temperature regulation (effects of 1 and 2) appears to explain why tits approach the raptor and vocalize much later than they physically can but at the cost of suboptimal escape in case of an attack. While the delay of calling can be understood as countering the risk of approaching closely (see above) the delay of coming at all cannot. A tit would be capable of coming within ca. 4 s. Both MD and LA seem to minimize risk as *anticipated* at the moment of hearing the onset of the stimulation. Also, hiding into cover (RI = −0) when the nestlings are still young must be ascribed to a *restraint*; in which case the bird refrains from putting its performance to a direct test in confrontation with the predator. Restraints are operating by anticipation of a constraint, namely to flee in case necessity arises. But there is danger in invoking constraints in this way before all contextual information is at hand. The dependency of the male's MD on the brood *and* the ♀ is evidence that constraints should not be invoked if the worth at stake is not known.

(3) Behaviour may be constrained by *lack of information*. Tits which had observed from cover a mobbing party around the owl for some time could afford to attain their MD more quickly (p. 135). Apparently these birds could assess their future risk imposed by their MD more accurately. We also found that tits (appear and call earlier and) approach the owl more rapidly (LMD) the farther away from danger safe cover was (Table 4, Fig. 2). This could mean that when hiding is not possible tits can only gather sufficient information by coming closer to look. Postponing this decision would make no sense and so they come earlier.

Tests of predictive sociobiology

Nestling age (7) and brood size (6) as determinants of defence behaviour. We have measured in a number of ways that great tits increase their brood

defence with nestling age (Fig. 2), though RI seems to diminish again with very old age. This means that great tits are capable of potentiating their multidimensional brood defence behaviour with nestling age as predicted by the theory as do many other altricial birds. Older broods would lead to greater efforts because the reproductive value of the nestlings increases monotonically with age so that their value for the parents rises correspondingly (Emlen 1970; Andersson et al. 1980). There is much evidence that parental defence efforts do *not* increase with the *number* of young, as predicted. Instead, an increase in brood size causes RI to *abate* where there is an effect at all. The depressing effect of brood size, if any, may be due to a constraint, e.g. fatigue of parents from feeding. The effects of nestling age and number cancel each other partly, for RI levels are prevented from rising with age in the largest broods (9–12).

However, constraint cannot be invoked safely to account for the lack of correlation of RI and brood size in young broods, since stress related to brood size should not matter much at that age. Furthermore, great tits *are* capable of increasing RI under the impact of another determinant, namely the age of the young. Theory views nestling number as a predictor of gain in future fitness (reproductive value) which alone should influence parental decision-making (Dawkins and Carlisle 1976). If theory is correct one has to conclude that great tits do not behave adaptively in this respect. They do have the required perceptual capacity for they are able to adjust their feeding rate to brood size (Gibb 1955; Perrins 1979). It is difficult to see why for brood defence they should not use a mechanism they have for measuring brood size or some suitable equivalent. In a pioneering study, Robertson and Biermann (1979) found an icterid to defend the nest against a dummy snake in proportion to the (manipulated) number of eggs, i.e. to the expected benefit, but not in proportion to the number of young. The failure of this icterid and the great tit to vary RI with the number of nestlings could be understood by assuming that parents would gauge their defence efforts to *past or future parental investment* in terms of energy output, not in terms of the number of nestlings tended. Such an explanation would require energy output as assessed by the parent to be independent of brood size, thus leaving the issue of the birds committing the Concorde Fallacy undecided (Weatherhead 1982 and in litt.). This assumes that all parents, regardless of the size of their brood, would be about equally strained, for which there is some evidence. Assuming that parents would gear parental efforts to past investment would ex-

plain both their insensitivity to brood size *and* their use of brood age as predictors of future benefits (for details see Curio 1983b).

Dilution of risk or attack interference? We were surprised to find that tits do not risk more with increasing numbers of mobbers as in the case of Panamanian forest birds (Regelmann et al., in preparation). Instead, the expected number of mobbers increases risk-prone behaviour as measured by two latency scores (Table 3). For reasons of measurement, only minimum distance (MD) could be examined in relation to the actual number of party members present. We cannot explain why we did not find any such relationship. In view of the female's potentiating influence on the ♂, the facilitatory effect exerted by the surrounding community cannot be any simple dilution of risk by numbers; alien birds keep on average farther away so that a parent tit would be the first victim in case of an attack. We tend to think that confusion or some other sort of attack interference due to numbers (Regelmann et al., in preparation) is exploited by the tits to their advantage.

Predictions from life history theory

Season (5) and year (15). As the season advances the prospects for starting a new brood or a second brood dwindle (Kluijver 1951; Perrins 1979). This implies that the value of the current brood increases compared with the residual reproductive value (Williams 1966; Curio and Regelmann 1982). Hence, parent tits should invest more into the current brood when the season advances. This is indeed suggested by the single year (1979) analysis of four different response measures. Contrary to expectation, the late season of the year 1979 exhibited a decrease of risk taken, evidenced by a longer LC than in the other years. Apparently, the incremental effect of a late season was confounded by unusually good food conditions in 1979, since nestling survival was exceptionally good. These favourable conditions may have been responsible for the fact that the expected reduction in the number of second broods occurred in 1979 in only some study areas. There were further annual differences in that only the 1980 tits behaved more 'risk-aversive' in at least two measures (LA, RI) which is possibly due to the unusually adverse weather conditions. Hence, energetic constraints may have been more important than evolved restraints.

Habitat (3). The proportion of great tits starting a second brood is larger in coniferous than broad-

leaved forests (Kluijver 1951; van Balen 1973; Perrins 1979). This suggests that, all other things being equal, tits should invest more into defence of first broods in broad-leaved habitat. In contrast, birds approached and vocalized there later (Fig. 2). In Bahrdorf where the proportion of Scots pine is most prominent, plots of pine and broad-leaved (mixed) forest form a rather fine-grained mosaic. This may mean that there are no true coniferous forest tits, since their territories are mostly within reach of other wood plots. Hence, the habitat difference found most probably reflects more proximate but as yet unknown causes.

References

Andersson M, Wiklund CG, Rundgren H (1980) Parental defence of offspring: a model and an example. Anim Behav 28:536–542

Balen JH van (1973) A comparative study of the breeding ecology of the great tit *Parus major* in different habitats. Ardea 61:1–93

Berndt R, Winkel W (1967) Die Gelegegröße des Trauerschnäppers (*Ficedula hypoleuca*) in Beziehung zu Ort, Zeit, Biotop und Alter. Vogelwelt 88:97–136

Beutel P (1980) Statistik-Programm-System für die Sozialwissenschaften: SPSS 8. Zahlreiche Tabellen und Beispiele von Beutel P, Küffner H, Schubö W. Nach Nie NH, Hull CH, 3rd edn. Fischer, Stuttgart New York

Bildstein KL (1982) Responses of northern harriers to mobbing passerines. J Field Ornithol 53:7–14

Chase ID (1980) Cooperative and noncooperative behavior in animals. Am Nat 115:827–857

Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: A study of avian visual perception. Anim Behav 23:1–115

Curio E (1978) The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. Z Tierpsychol 48:175–183

Curio E (1980) An unknown determinant of a sex-specific altruism. Z Tierpsychol 53:139–152

Curio E (1983a) Time-energy-budgets and optimization. Experientia 39:25–34

Curio E (1983b) Begehen Kohlmeisen den Concorde-Fehler? J Ornithol 124:196–198

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

Curio E, Augst HJ, Böcking HW, Milinski M, Ohguchi O (1978) Wie Singvögel auf Feindrufe hassen lernen. J Ornithol 119:231–233

Dawkins R, Carlisle TR (1976) Parental investment, mate desertion and a fallacy. Nature 262:131–133

Dooling RJ (1980) Behavior and psychophysics of hearing in birds. In: Popper AN, Fay RR (eds) Proceedings in life sciences. Comparative studies of hearing in vertebrates. Springer, Berlin Heidelberg New York, pp 261–288

Emlen JM (1970) Age specificity and ecological theory. Ecology 51:588–601

Gaensslen H, Schuboe W (1976) Einfache und komplexe statistische Analyse. Reinhardt, München Basel

Gibb J (1955) Feeding rates of great tits. Br Birds 48:49–58

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Herzog K (1968) Anatomie und Flugbiologie der Vögel. Fischer, Stuttgart

Hinde RA (1952) The behaviour of the great tit (*Parus major*) and some other related species. Behav (Suppl II) 1–201

Kluijver HN (1950) Daily routines of the great tit, *Parus major* L. Ardea 38:99–135

Kluijver HN (1951) The population of the great tit, *Parus major* L. Ardea 39:1–135

Latimer W (1977) A comparative study of the songs and alarm calls of some *Parus* species. Z Tierpsychol 45:414–433

Marten K, Marler P (1977) Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav Ecol Sociobiol 2:271–290

Nomoto S, Rautenberg W, Iriki M (1983) Temperature regulation during exercise in the Japanese quail (*Coturnix coturnix japonica*). J Comp Physiol 149:519–525

Perrins CM (1979) British tits. Collins, London

Robertson RJ, Biermann GC (1979) Parental investment strategies determined by expected benefits. Z Tierpsychol 50:124–128

Shalter MD (1979) Responses of nesting passerines to alarm calls. Ibis 121:362–368

Shedd DH (1982) Seasonal variation and function of mobbing and related antipredator behaviors of the American robin (*Turdus migratorius*). Auk 99:342–346

Smith JNM, Sweatman HPA (1974) Food-searching behaviour of titmice in patchy environments. Ecology 55:1216–1232

Sokal RR, Rohlf JF (1981) Biometry: The principles and practice of statistics in biological research, 2nd edn. Freeman, San Francisco, pp 617–778

Stearns SC (1976) Life-history tactics: a review of the ideas. Q Rev Biol 51:3–47

Weatherhead PJ (1982) Risk-taking by red-winged blackbirds and the Concorde Fallacy. Z Tierpsychol 60:199–208

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690

Winkel W (1970) Hinweise zur Art- und Altersbestimmung von Nestlingen höhlenbrütender Vogelarten anhand ihrer Körperentwicklung. Vogelwelt 91:52–59

Winkel W, Winkel D (1981) Zum Paarzusammenhalt bei Kohl-, Blau- und Tannenmeise (*Parus major, P. caeruleus* und *P. ater*). Vogelwarte 30:325–333