Biologia, Bratislava, **56**/5: 549—556, 2001

Differences in behaviour of closely related thrushes (*Turdus philomelos* and *T. merula*) to experimental parasitism by the common cuckoo *Cuculus canorus*

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Grim, T. & Honza, M., Differences in behaviour of closely related thrushes (*Turdus philomelos* and *T. merula*) towards experimental parasitism by the common cuckoo *Cuculus canorus*. Biologia, Bratislava, **56:** 549—556, 2001; ISSN 0006-3088.

The common cuckoo *Cuculus canorus* parasitizes many passerines, but some common species sympatric with the brood parasite are rarely used as hosts. Potential host species may escape brood parasitism using methods such as high rejection of cuckoo eggs or high aggressiveness towards female parasite. We tested the responses of two common species, the song thrush *Turdus philomelos* and blackbird *T. merula*, not regularly parasitised by the cuckoo, to artificial cuckoo eggs and dummies. Both species rejected model parasitic eggs (song thrush 58.3%, blackbird 66.7%). Song thrushes showed very low levels of aggression toward a stuffed dummy, while blackbirds were very aggressive. Neither species discriminated between the cuckoo and control pigeon dummies. We observed one case of intraspecific nest parasitism in the song thrush. This is probably the first documentation of intraspecific nest parasitism in this species. Both our and previously published data indicate that the rejection behaviour of *Turdus* species evolved as a defence against intraspecific nest parasitism. This behaviour contributes to cuckoos avoiding these potential host species. However, other nonexclusive factors (e.g. diet composition) could explain more fully why thrushes are not victimized by the cuckoo.

Key words: brood parasitism, nest defence, mimicry, aggression, co-evolution, egg rejection.

Introduction

The common cuckoo *Cuculus canorus* (Linnaeus, 1758) is a brood parasite whose eggs have been found in nests of more than one hundred species of small passerines (Moksnes & Røskaft, 1995). However, only five to ten host species are parasitised regularly (Rothstein & Robinson, 1998). Other common species of open-nesting passerines sympatric with the cuckoo (e.g. *Turdus, Emberiza, Carduelis*) are parasitised rarely or not at all (Moksnes & Røskaft, 1995).

Although brood parasitism by the cuckoo and its North-American counterpart, the brown-headed cowbird *Molothrus ater* (Boddaert, 1783) is currently subject to intensive research (for reviews see ORTEGA, 1998; ROTHSTEIN & ROBINSON, 1998), few authors have tried to explain low levels of parasitism in particular host species. DAVIES & BROOKE (1989) and MOKSNES & RØSKAFT (1992) found that several rare cuckoo hosts (e.g. the reed bunting *Emberiza schoeniclus* Linnaeus, 1758 and willow warbler *Phylloscopus trochilus* Linnaeus, 1758) show fine egg discrimination. PEER & BOLLINGER (1997) reported that low synchronization between breeding cycles of the host (common grackles *Quiscalus quiscula* Linnaeus, 1758) and parasite (brown-headed cowbirds) is responsible for low parasitism rates in common grackles. Brown-headed cowbirds avoid parasitising eastern kingbirds *Tyrannus tyrannus* (Linnaeus, 1758) because their eggs would be wasted – kingbirds reject almost 100% of parasitic eggs (SEALY & BAZIN, 1995). MERMOZ & FERNANDÉZ (1999) explained the low frequency of parasitism in scarlet-headed blackbirds *Amblyramphus holosericeus* (Scopoli, 1786) by shiny cowbirds *Molothrus bonariensis* (Gmelin, 1789) with the fact that the scarlet-headed blackbird shows a high level of nest attentiveness and therefore the parasitic female cannot lay without being noticed and attacked by the nest owners.

Several hypotheses were proposed to explain why a particular bird species is not victimized by a brood parasite including host breeding success, egg acceptance/rejection status, intensity of nest defence, host care and diet, nest type and habitat (ORTEGA, 1998). In this paper we test two of these hypotheses (egg rejection and nest defence) in two common passerines: the song thrush *Turdus philomelos* (C.L. Brehm, 1831), and blackbird *T. merula* (Linnaeus, 1758). Observations of parasitism in the two species are extremely rare. LACK (1963) reported only 3 parasitized nests among 22,656 blackbird nests in England. MOKSNES & RØSKAFT (1995) found only 11 and 21 cuckoo eggs laid in the nests of the two respective species ($n = 11,870$ clutches of European passerines held in museum egg-collections). In addition, none of these cuckoo eggs matched the eggs of the song thrush and blackbird in appearance. These data indicate that neither species are regularly used as fosterers by the common cuckoo.

KLEVEN et al. (1999) found that the size of the host had a significant effect on the growth of cuckoo nestlings – cuckoo chicks cared for by larger host species, such as the great reed warbler *Acrocephalus arundinaceus* (Linnaeus, 1758), were significantly heavier at fledging than nestlings raised by a smaller host, the reed warbler *Acrocephalus scirpaceus* (Hermann, 1804). In the light of this finding it is interesting that no *Turdus* species is regularly used as a host by the cuckoo despite the body size of these potential hosts.

Therefore we made an attempt to explain why the song thrush and blackbird are not parasitised by the common cuckoo. Responses of the two species to parasitic eggs were tested only in Great Britain (DAVIES & BROOKE, 1989) and Norway (MOKSNES et al., 1990). We focused on nest defence behaviour and parasite recognition abilities of the song thrush and blackbird, which have not been studied, to date.

Methods

The study was conducted in a deciduous forest nearby Dolní Bojanovice village (48°52′ N, 17°00′ E), about 60 km SE of Brno, South Moravia, Czech Republic. Data were collected from 25 April to 30 June 2000 and 2001.

For the egg experiments we used natural Chinese quail *Coturnix chinensis* (Linnaeus, 1766) eggs painted blue to mimic eggs of the cuckoo gent parasitising the redstart *Phoenicurus phoenicurus* (Linnaeus, 1758) (MOKSNES & RØSKAFT, 1995). We introduced experimental eggs to "host" nests at the egg-laying or early incubation stages (from day 2 till day 6; day 0 is the day when the first egg was laid; the clutch size in both species tested is 3–5; CRAMP, 1988). To minimize disturbance to the hosts, we did not remove any host eggs (as female cuckoos do) because the experimental removal of one host egg has no effect on the rejection rates of model eggs (DAVIES & BROOKE, 1989). We experimentally parasitised 17 song thrush and 8 blackbird nests. The egg was considered accepted if it remained in the nest for six days. This criterion is used because almost all observed rejections in different host species appeared before the sixth day after the egg was introduced, see e.g. MOKSNES et al. (1990); DAVIES & BROOKE (1989) reported that most rejections took place within 3 days after clutch completion.

Nest defence by hosts was tested with stuffed dummies of the common cuckoo and the feral pigeon *Columba livia f. domestica* (Gmelin, 1789) as a control. We chose the pigeon as a control species because it is about the same size and shape as a cuckoo but provides no threat to the either species tested. The experimental design followed the standard procedure suggested by SEALY et al. (1998). First, one of dummies (in a life-like position) was attached to a branch about 0.5 m from a focal nest. The head of the dummy was directed to the nest. After the first parent appeared near the nest and became aware of the dummy, reactions of nest owners were observed for 5 min from a hide set up 20 m from the focal nest. Presentation of the second mount at the same place was separated by a 30 min interval to avoid habituation or carry-over aggression (SEALY et al., 1998). The order in which models

Table 1. The outcome of the observed nesting attempts and results of model egg experiments at song thrush and blackbird nests. There were no significant interspecific differences in all measured outcomes (chi-square and Fisher's exact probabilities tests, all n.s.).

Outcome	Song thrush ($n = 55$)		Blackbird ($n = 25$)	
	Control	Experiment	Control	Experiment
Predated	27/38	5/17	12/17	2/8
Experimental egg accepted	–	5/12	–	2/6
Experimental egg ejected	–	4/12	–	3/6
Nest deserted	0/38	3/12	0/17	1/6

Note: some of successful experimental nests were predated after the egg experiments finished, therefore the breeding success is actually lower than is shown in the table as noted in the results.

were presented was randomized. All experiments with stuffed dummies were performed by one author (T.G.) to avoid possible observer bias. The number of nests tested was 15 for the song thrush and 6 for the blackbird. In the song thrush 6 nests were tested at the egg stage and 9 at the nestling stage, while all blackbird nests were tested at the nestling stage.

The intensity of nest defence varied from quiet watching of the nest from a distance to vigorous mobbing of the dummy. We adjusted our categorization of host responses to natural variation in responses observed during our experiments. Blackbirds usually quickly attacked the mount directly (the mount was immediately removed to avoid its destruction), so we did not quantify host reactions as a number of particular behaviours per 5 min of observation. Instead, we quantified the behaviour of both blackbirds and song thrushes on relative subjective scales (see e.g. Mermoz & Fernández, 1999). We recorded the behavioural variables suggested by Sealy et al. (1998) to enable interspecific comparisons (see e.g. Gill et al., 1997). We measured the delay in arrival of nest owners from the moment the dummy was attached near the focal nest (latency of response) in minutes, which should reflect the general level of nest attentiveness. Latency in response can be taken as a rough measure of time the parents spent at the nest which is crucial with respect to interaction with the brood parasitic cuckoo which lays extremely quickly to avoid host attacks. In addition we quantified several parameters of host reactions: vocalizations (0 to 3, i.e. from no vocalizations to very strong and permanent vocalizations), contact attacks (0 = none, 1 = one or more), overall level of response (0 = no response, i.e. silent watching of a dummy, 1 = few vocalizations, bird(s) usually more than 10 m from the dummy, 2 = more vocalizations, bird usually less than 10 m from the dummy, 3 = strong vocalizations and close passes, 4 = strong vocalizations and contact attacks). These parameters should reflect the risks taken by birds when defending their nests. Each nest was tested only once to avoid pseudoreplication.

Results

Egg discrimination

Altogether we observed 66 song thrush and 31 blackbird nesting attempts (11 song thrush and 6 blackbird nests were not followed to fledging and their final fate is unknown). The proportions of successful breeding attempts (nests with a known fate) of song thrushes (41.8%, $n = 55$) and blackbirds (44.0%, $n = 25$) were not statistically significantly different ($\chi^2 = 0.0003$, d.f. = 1, $P = 0.85$). The main reason for nesting failure was the predation of clutch (Tab. 1).

We experimentally parasitised 17 song thrush and 8 blackbird nests and only 12 and 6 artificially parasitised nests survived the 6 days acceptance/rejection criterion, for each species respectively. Song thrushes rejected 58.3% and blackbirds 66.7% of parasitic eggs (Tab. 1). Rejection methods used by both species were ejection of the parasite egg and desertion of the parasitised nest (Tab. 1). Blackbirds rejected parasitic eggs more quickly than song thrushes (medians: 1 and 4 days; Mann-Whitney test, $Z = 2.038$, $P = 0.040$, $n = 7$). At three predated song thrush nests the parasitic eggs were accepted for 1, 2 and 4 days before predation of the clutch (the remaining 2 nests were predated before the first check). At predated blackbird nests the parasitic eggs remained in the nests for 1 and 3 days before being predated. One song thrush and one blackbird deserted their experimentally parasitised nests. Both desertions occurred less than three days after the parasitic egg was added. This behaviour is probably a response to parasitism as no control nests (which were regularly checked but not used in experiments) were deserted.

We observed one case of intraspecific nest parasitism in the song thrush. The parasitic egg

Table 2. Intraspecific comparison of intensity of song thrush and blackbird responses to cuckoo and pigeon dummies. Values are medians. There were no differences in responses to the two types of dummies in both host species in any of the measured behavioural parameters (Wilcoxon matched pairs tests, all n.s.). Latency of response was measured in minutes, other parameters measured on ordinal scale (see Methods).

Parameter	Song thrush ($n = 15$)		Blackbird ($n = 6$)	
	Cuckoo	Pigeon	Cuckoo	Pigeon
Latency of response	7	8	12	6
Vocalizations	1	1	2	1
Contacts	0	0	1	1
Overall level of nest defence	1	1	4	4

Table 3. Interspecific comparison of intensity of song thrush and blackbird responses to stuffed dummies. Values are medians. The results of Mann-Whitney tests are shown. Latency of response was measured in minutes, other parameters measured on ordinal scale (see Methods). Differences which remained significant after sequential Bonferroni test (RICE, 1989) are indicated with an asterisk ($P < 0.05$).

Parameter	Song thrush ($n = 15$)	Blackbird ($n = 6$)	Z	P
Latency of response	7	9	1.686	n.s.
Vocalizations	1	2	2.352	*
Contacts	0	1	2.335	*
Overall level of nest defence	1	4	2.182	*

was laid seven days after the host clutch completion (the appearance of eggs both before and after the host's laying period is considered as an indication of brood parasitism, see e.g. RINGSBY et al., 1993). Five days later the parasitic egg was destroyed due to partial predation of the clutch. As far as we know, this is the first observation of intraspecific brood parasitism in the song thrush.

Nest defence

We found no differences in song thrush responses to mounts between the egg ($n = 6$) and nestling ($n = 9$) stage in latency of response, vocalizations, contacts and overall level of nest defence (Mann-Whitney tests, $P > 0.05$ in all cases). Therefore the data were pooled. Neither song thrushes or blackbirds distinguished between the cuckoo and the control species – there were no differences between the responses of either species to either type of dummy in any of the measured behavioural parameters (Wilcoxon matched pairs tests, all n.s.; Tab. 2). There was no relationship between the latency of response and overall level of nest defence (song thrush: $r_s = -0.355$, $P = 0.194$, $n = 15$; blackbird: $r_s = 0.655$, $P = 0.158$, $n = 6$). The number of attacking individuals had no effect on the overall level of aggression in the song thrush (Mann-Whitney test, $Z = 1.687$, $P = 0.092$, $n = 15$). Interestingly, during five experiments on blackbirds the overall level of aggression was highest (level 4) and both parents attacked a dummy together in all five cases. In one experiment only the female was present showing no aggression at all. The male was never observed at this nest. This female also accepted the experimental blue egg, which remained in the nest for 15 days and was not ejected even after nestlings hatched.

There were no significant differences in the latency of response between species (Tab. 3). However, the number of individuals performing nest defence behaviour differed between species – in the song thrush usually only one parent responded, but in the blackbird both male and female attacked dummies (Fisher's exact probabilities test, $P = 0.046$). Moreover, blackbirds vocalized more strongly, attacked the mount directly with higher a probability and showed higher overall level of nest defence than song thrushes (Tab. 3). Song thrushes responded very weakly to dummies. They usually stayed more than 10 meters from the nest uttering very few vocalizations about 20 times per 5 min observation period. Comparable data for blackbirds are lacking because blackbirds uttered alarm calls very quickly and almost continuously, moreover, the nest owners immediately attacked the mount directly and therefore the experiments were stopped earlier thus making sensible interspecific comparison of call rates impossible (see Methods). Only two studied song thrushes responded extremely aggressively and one even showed redirected aggression towards its own nest (this unusual observation is described in detail by GRIM, 2000). On the other hand, blackbirds behaved very aggressively – they continually and intensively vocalized and mobbed dummies vigorously. In conclusion, the low level of song thrush nest defence would present almost no risk to a female cuckoo. On the other hand, the extremely vigorous nest defence behaviour shown by blackbirds would threaten a female cuckoo's life.

Three song thrush and three blackbird nests were tested with both parasitic eggs and dummies. Dummy experiments were performed after the egg experiments finished. Parents in four nests accepted parasitic eggs. It might be expected that acceptors are naive breeders (LOTEM et al., 1992) that would also defend their nests poorly. However, intensity of response to mounts was at levels 1 and 2 for the two song thrush nests and 0 and 4 for the two blackbird nests. Parasitic eggs were rejected at two other nests. Intensity of response to dummies was at level 1 for one song thrush nest and 4 for the blackbird nest. Our data sets are too small to be analysed statistically, however, they show some inconsistency in the host responses to eggs versus dummies.

Discussion

Egg discrimination

The breeding success of the study species found during our study seasons (song thrush: 41.8%, blackbird: 44.0%) is similar to that found in previous studies (e.g. OSBORNE & OSBORNE, 1980; HATCHWELL et al., 1996). It is within the range of breeding success of bird species commonly used as hosts by the cuckoo. Therefore the level of breeding success in the song thrush and blackbird probably has no effect on the avoidance of these species by the cuckoo.

The results of the egg experiments are similar to those reported by DAVIES & BROOKE (1989). They found that song thrushes rejected 27.3% and blackbirds 59.1% of non-mimetic redstart type eggs (i.e. the same type as we used in our study). Overall levels of rejection of several types of alien eggs by song thrushes and blackbirds were 58.5% and 61.8% respectively (DAVIES & BROOKE, 1989). These values are higher than the rejection rates of commonly parasitised hosts (DAVIES & BROOKE, 1989). In a study by MOKSNES et al. (1990) 20% of song thrush pairs rejected a model cuckoo egg and two blackbirds also rejected them. Four experimentally parasitised nests in our study were deserted. We consider this as a method of rejection because DAVIES & BROOKE (1989) showed that desertion can serve as a method of rejection – hosts tested by them deserted nests parasitised with non-mimetic eggs more frequently then nests parasitised with mimetic eggs.

The cuckoo probably does not use some hosts (e.g. the reed bunting and spotted flycatcher *Muscicapa striata* Pallas 1764) because they show high rejection rates of parasitic eggs (DAVIES & BROOKE, 1989). However, great reed warblers *Acrocephalus arundinaceus* in Hungary reject 39% of cuckoo eggs and are still heavily parasitised (MOSKÁT & HONZA, 2000). Other commonly used hosts are also rejecters (DAVIES & BROOKE, 1989). Our data and the results of DAVIES & BROOKE (1989) and MOKSNES et al. (1990) show that both the song thrush and blackbird can recognize and reject parasitic eggs. However, these studies also indicate that the egg rejection behaviour of the song thrush and blackbird cannot alone explain the low level of parasitism in these species.

We documented one case of intraspecific nest parasitism in the song thrush. We found no other report on intraspecific nest parasitism by the song thrush in the literature. However, GRENDSTAD et al. (1999) reported that one of the studied redwing *Turdus iliacus* (Linnaeus, 1766) nests was parasitized by the closely related fieldfare *Turdus pilaris* (Linnaeus, 1758). Interestingly, RINGSBY et al. (1993) detected a relatively high intraspecific parasitism rate in fieldfares (11.5%). Redwings discriminate against intraspecific eggs introduced to their nests and show stronger aggression toward conspecific compared to the female cuckoo. This strongly suggests that redwings evolved this behaviour as a defence against intraspecific and not interspecific nest parasitism (GRENDSTAD et al., 1999).

Nest defence

Blackbirds displayed aggressive nest defence behaviour and readily attacked dummies with contact. The blackbird is generally very aggressive and intraspecific fights can lead to death (CRAMP, 1988). Its parental anti-predatory behaviour is also reported to be very intense (CRAMP, 1988). The song thrush is similarly described as aggressive by

CRAMP (1988), however, in our study only two of 15 tested pairs attacked the dummy directly and the overall level of aggressiveness was very low compared to the blackbird.

We found that both studied species did not discriminate between the cuckoo and control pigeon mounts. This result indicates that the behaviour of song thrushes and blackbirds was a result of generalized nest defence and not a response to a specific threat provided by the parasite. However, DUCKWORTH (1991) found that reed warblers *Acrocephalus scirpaceus* (commonly parasitised by the cuckoo throughout their range) can differentiate cuckoos from similar sparrowhawks *Accipiter nisus* (Linnaeus, 1758). The reed warbler's response was more aggressive to a cuckoo than to a sparrowhawk during incubation, but the reaction to the cuckoo disappeared after fledging although the parents still responded strongly to a sparrowhawk at that stage. Therefore our results indicate that there probably was no co-evolutionary arms-race between the cuckoo and *Turdus* species. This hypothesis is supported by the fact that none of the cuckoo eggs found in song thrush and blackbird nests were mimicking host species eggs (MOKSNES & RØSKAFT, 1995). Fieldfares show aggression towards a hooded crow *Corvus corone* (Linnaeus, 1758) dummy (MEILVANG et al., 1997) but they do not consider the cuckoo to be a potential threat (MOKSNES & RØSKAFT, 1988). GRENDSTAD et al. (1999) also concluded that redwings evolved alien egg rejection as a defence against intraspecific brood parasitism. We observed one case of intraspecific nest parasitism in the song thrush which also gives support to the hypothesis that *Turdus* species have not been in the co-evolutionary arms race with the cuckoo.

The overall level of nest defence by song thrushes was very low. Thus, the song thrush would not prevent a female cuckoo trying to lay an egg in a song thrush nest. However, the very high intensity of blackbird aggression suggests that the cuckoo would risk serious injury if attacked at a blackbird nest during the parasitism act. MOLNÁR (1944) reported several observations of dead female cuckoos under great reed warbler nests. Females were evidently killed by the nest owners. The blackbird is a much larger bird than the great reed warbler (100 g vs 30 g), thus, a female cuckoo would probably risk much more at a blackbird than warbler nest. The poor level of nest defence shown by the song thrush and strong aggression shown by blackbirds in our study are consistent with the results of dummy experiments performed by V. BIČÍK in Czech Republic (unpublished data; in verb).

MERMOZ & FERNÁNDEZ (1999) described a low rate of parasitism in scarlet-headed blackbirds *Amblyramphus holosericeus* with a non-specific life-history trait, i.e. high levels of nest attentiveness combined with aggressive host behaviour against all intruders. Scarlet-headed blackbirds do not recognize the shiny cowbird *Molothrus bonariensis* as a specific threat, but 98% of time the nest is guarded by at least one parent. The high level of nest attentiveness cannot play an important role in the cuckoo's avoidance of blackbirds and song thrushes as these species arrive at their nest with long delays (Tabs 1, 2), i.e. nest attentiveness is very poor and the probability of encountering a brood parasite at the host nest is consequently minimal.

We tested whether the cuckoo avoids parasitising song thrush and blackbird nests because these species have low breeding success, strong egg rejection behaviour or intensive nest defence. We found that both species discriminated parasitic non-mimetic eggs. Moreover, blackbirds, although they do not recognize the female cuckoo as a specific threat (they attacked the pigeon with the same vigour), have a high level of generalized nest defence that could threaten the female cuckoo. However, both these behaviours are shared with commonly parasitised hosts (e.g. *Phylloscopus* warblers or the great reed warbler are also strongly aggressive to the cuckoo). Thus, these factors cannot alone explain why cuckoos avoid parasitising them.

ORTEGA (1998) presents 12 hypotheses trying to explain the absence of parasitism in some passerine species. It is unlikely that most of these could explain the avoidance of *Turdus* species specifically (e.g. short host incubation period, insufficient amount of parental care, unsuitable habitat, well concealed hosts nests). However, other hypotheses are more likely to explain the absence of parasitism in thrushes. MOKSNES & RØSKAFT (1988) hypothesized that *Turdus* nests could be too deep for a cuckoo nestling to evict host eggs or nestlings. However, MOKSNES et al. (1990) reported an observation of a four-day old cuckoo chick ejecting a fieldfare nestling weighing 10.0 g. *Turdus* nestlings grow very quickly (CRAMP, 1988), thus cuckoo nestling could have big problems competing with host chicks. In addition, cuckoos and cowbirds can live only on an insectivorous diet. Their breeding success in nests of granivorous birds is very low – diet composition sufficiently explains the absence of parasitism in e.g. greenfinch *Carduelis chloris* (Linnaeus, 1758), linnet *C. cannabina* (Linnaeus, 1758) and bullfinch *Pyrrhula pyrrhula* (Linnaeus, 1758) (DAVIES & BROOKE, 1989). The song thrush and blackbird feed their nestlings mainly on molluscs and earthworms respectively (CRAMP, 1988). These food items are probably indigestible for the cuckoo nestling that must be brought up on insects. However, this hypothesis could be rigorously tested only by cross-fostering experiments, i.e. transferring nestling cuckoos to *Turdus* nests. In a preliminary experiment it was found that a cuckoo nestling did not survive in a blackbird nest.

In conclusion, our results suggest that the intensity of antiparasitic behaviour shown by song thrushes probably has a low effect on brood parasite choice. However, strong generalized nest defence by blackbirds probably constrains the use of this species by the cuckoo, although the low level of nest attentiveness in this species reduces the benefits of strong nest defence. Nevertheless, other hypotheses (food, nest type) need testing before decisive conclusions can be drawn. Our observations, coupled with previous findings, support the hypothesis that *Turdus* species have evolved rejection behaviour against intraspecific nest parasitism.

Acknowledgements

We are grateful to M. ČAPEK, V. MRLÍK and P. PROCHÁZKA for their help during the field work. Suggestions by two anonymous referees substantially improved the MS. The research was supported by Palacký University internal grant (no. 3210–3013) operated to T. GRIM and grant 206/00/P046 operated to M. HONZA.

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Received November 14, 2000
Accepted June 6, 2001