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Nest defence, enemy recognition and nest inspection behaviour of experimentally parasitized Reed Warblers *Acrocephalus scirpaceus*

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Capsule Reed Warblers in a regularly parasitized population do not recognize Cuckoo *Cuculus canorus* as a special enemy and do not change their behaviour at nest immediately after being parasitized.

Aims To assess if an intruder near the nest influences the behaviour of the Cuckoo host.

Methods Host responses to Cuckoo, control Pigeon dummies and human intruder were observed. Host behaviour at 71 nests was video-recorded for 30 minutes at four experimental groups of nests: Cuckoo dummy, Cuckoo dummy + Cuckoo egg, Pigeon dummy, human intruder.

Results Reed Warblers did not respond differently to the Cuckoo and the control species. The experimental procedure had no significant effect on the behaviour of hosts during the study period. We were unable to find any differences in the time spent at the nest, clutch inspection behaviour and nest defence behaviour between morning and afternoon experimental groups. Our results do not support the hypothesis that afternoon laying by the Cuckoo is maintained by a selection pressure from the host. We observed no ejection or egg-pecking during the 30-min period after the experimental parasitism.

Conclusions Low aggression and non-specificity of host responses in our study area are in line with the fact that the Reed Warbler is an intermediate rejecter of Cuckoo eggs as expected from the spatial habitat structure hypothesis.

One important factor affecting reproductive success and consequently nest defence behaviour in many passerine birds is brood parasitism (Rothstein 1990), because the successful act of parasitism often reduces host fitness dramatically. Clearly, the best protection for a host against parasitism is to avoid being parasitized. Hosts can avoid parasitism by breeding in safe sites (Alvarez 1993, Øien *et al.* 1996, Honza *et al.* 1998, Moskát & Honza 2000, Clarke *et al.* 2001) or by a vigorous nest defence (Moksnes *et al.* 1990, Sealy *et al.* 1998, Grim & Honza 2001, Røskaft *et al.* 2002b). There is a huge interspecific variation in defensive behaviour of potential host species against territory intruders. Some host species discriminate between the parasite and control species that pose no threat to them (Burgham & Picman 1989, Moksnes *et al.* 1993a) and some hosts also respond differently to brood parasites and predators (Duckworth 1991, Gill & Sealy 1996).

Cuckoo *Cuculus canorus* hosts that reject at very high frequencies show little variation in their defence behaviour (Øien *et al.* 1999). Variation in the aggressive response of a host to the parasite is influenced by various factors, e.g. by an occurrence of Cuckoos in the particular locality (hosts breeding in sympatry with the parasite are more aggressive than those breeding in allopatry; Røskaft *et al.* 2002b). Habitat selection by the host also plays an important role – host species breeding near trees only (Cuckoo vantage points) are more aggressive against a Cuckoo dummy and reject parasitic eggs at higher rates than host species breeding both near and further away from trees (Røskaft *et al.* 2002b, 2002c) probably because of gene flow between parasitized (near trees) and unparasitized (farther away from trees) populations.

In the case where a host is not successful in deterring

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*Correspondence author. Email: honza@brno.cas.cz a brood parasite, it is adaptive to recognize and reject the parasitic egg (Rothstein 1990). There are great differences in reactions of various hosts towards parasitic eggs. Cuckoo hosts normally exhibit some delay in their response towards the parasitic egg (Davies & Brooke 1988, Moksnes *et al.* 1990, Amundsen *et al.* 2002), but Moksnes *et al.* (1994) and Soler *et al.* (2003) documented relatively short times to ejection in Chaffinches *Fringilla coelebs*, Blackcaps *Sylvia atricapilla*, Sub-Alpine Warblers *S. cantillans* and Blackbirds *Turdus merula*.

Only a few studies have paid any attention to host behaviour immediately after the act of experimental Cuckoo parasitism: Moksnes *et al.* (1994) observed rejection behaviour of Chaffinches and Blackcaps and Martín-Vivaldi *et al.* (2002) video-recorded behaviour of three potential Cuckoo hosts to determine the effort needed to puncture experimentally added parasitic eggs (see also Soler *et al.* 2003). To our knowledge only one study has focused on host clutch inspection behaviour after the presentation of a stuffed Cuckoo dummy (Moksnes *et al.* 1993a). On the other hand several studies have been conducted on hosts of Brown-headed Cowbird *Molothrus ater* immediately after the act of parasitism (Rothstein 1977, Briskie & Sealy 1987, Sealy & Neudorf 1995, Sealy 1996, Sealy & Lorenzana 1998). Most of these studies did not, however, examine host behaviour in detail. More importantly, in all these studies (except Moksnes *et al.* 1993a) only experimentally parasitized nests were observed and there were no observations of unparasitized control nests. This makes a general interpretation of the results difficult because of problems of separating specific responses to parasitism and general nest defence behaviour.

The Reed Warbler *Acrocephalus scirpaceus* is one of the most frequently used Cuckoo hosts in Europe (Moksnes & Røskaft 1995). However, the Reed Warbler is not very aggressive towards the Cuckoo (Duckworth 1991, Lindholm & Thomas 2000, Røskaft *et al.* 2002a, 2002b). We investigated whether host behaviour at the nest is influenced by the type of intruder (parasitic Cuckoo versus non-threatening intruder) during the presence of the intruder and also after it leaves the vicinity of the nest. As a more detailed knowledge of changes in all aspects of host behaviour during the course of a day is essential to understand parasitic adaptations of the Cuckoo (see also Moksnes *et al.* 2000) we performed experiments both in the morning and in the afternoon. We report behaviour of Reed Warblers in detail with respect to the time of day and the kind of intruder, immediately after nests have been tested experimentally.

We made the following predictions. (1) If hosts can distinguish between their enemies and non-enemies, they should respond with higher intensity of nest defence to a brood parasite than to control dummies of a non-threatening species. Nest defence could be performed either as aggression (see Moksnes *et al.* 1990) or sitting in the nest to prevent parasites access to the nest (see Hobson & Sealy 1989). We predicted that Reed Warblers would show a higher level of nest defence towards a Cuckoo dummy than to a non-threatening species. (2) The presence of a stuffed Cuckoo dummy in close proximity to the nest is reported to facilitate host egg discrimination behaviour (Davies & Brooke 1988, Moksnes & Røskaft 1989, Moksnes *et al.* 2000), i.e. a Cuckoo dummy increases the likelihood that a host will reject a Cuckoo egg. We therefore predicted that hosts should show a higher intensity of clutch inspection behaviour after being faced with a Cuckoo dummy compared with a non-threatening control species. (3) The Cuckoo, unlike its hosts, lays its eggs in the afternoon (Wyllie 1981; but see Honza *et al.* 2002). Davies & Brooke (1988) suggested that this behaviour has evolved because the Cuckoo has a lower probability of encountering hosts during the parasitism act in the afternoon. Such behaviour should be adaptive because a physical presence of the host at its nest can serve as an effective defence against successful parasitism (Hobson & Sealy 1989; however, Moksnes *et al.* 2000 found no support for this hypothesis). Alternative explanations for the unique laying pattern of the Cuckoo are that hosts spend more time inspecting their clutches in the morning than in the afternoon (Davies & Brooke 1988) or they are more aggressive in the morning.

MATERIALS AND METHODS

Study area and fieldwork

The study sites were two pond systems in the south-eastern part of the Czech Republic near Lednice (48°48′N, 16°48′E) and Luzice (48°51′N, 17°04′E). The two systems are 25 km apart. We searched systematically for Reed Warbler nests in the littoral vegetation during the breeding periods between 15 May and 30 June in 1997 and 1998. We located nests in vegetation consisting mostly of Common Reed *Phragmites australis* and to a lesser extent of Reedmace *Typha angustifolia* surrounding the ponds. The fish ponds are situated in flat agricultural lowland landscape and are mostly surrounded by deciduous woods (see Hudec 1975 and Moksnes *et al.* 1993b, for more detailed descriptions of the study area).

The frequency of Cuckoo parasitism in Reed Warbler nests in our study areas is 15.0% (Øien *et al.* 1998) and Reed Warblers reject 37.5% of parasitic eggs (29.9% by desertion, 7.6% by ejection; Øien *et al.* 1998).

Experimental procedure and video recordings

We conducted experiments on nests during the egg-laying period (after the host had laid three or four eggs) to mimic a natural Cuckoo laying. A total of 71 nests was tested out of which 35 were tested during the morning (05:00–08:00 hours Central European Time, CET) and 36 during the afternoon (15:00–20:00 hours CET). To standardize our procedure, experiments were not conducted during rainy or windy days.

We established four experimental groups. (1) Cuckoo dummy group (n = 30). The Cuckoo dummy was presented 1 m from the nest. (2) Cuckoo dummy + Cuckoo egg group (n = 11). After the presentation of the Cuckoo dummy, the nest was experimentally parasitized with a real Cuckoo egg from the study area resembling the eggs of the Great Reed Warbler *Acrocephalus arundinaceus* (the egg was removed after the video recording was finished, see later). (3) Pigeon *Columba livia f. domestica* group (n = 16). The nest owner's reactions were tested with a stuffed Pigeon as a control non-threatening species. (4) Human intruder group (n = 14). One researcher (M.H.) as a control only visited the nest. Each nest was tested only once (i.e. one type of experiment) to avoid pseudoreplication.

To reduce the number of confounding variables (size, plumage colour, shape of a bird), we used Pigeon as the control species because its size and overall colour (grey) is similar to Cuckoo and it poses no threat to Reed Warblers (see also Sealy *et al.* 1998). Some researchers have used control species that are familiar to tested hosts (Moksnes & Røskaft 1989, Grim & Honza 2001), while others performed experiments with model species not occurring in the study area (Bazin & Sealy 1993). The Pigeon lives in sympatry with the Cuckoo in the nearest vicinity of reedbeds in our study area, therefore Reed Warblers probably have had a chance to gain prior experience with this species. Nevertheless, Sealy *et al.* (1998) suggested that prior experience (or its absence) with a control species should have no effect. The human intruder experiment was used to ascertain if responses to dummies are specific reactions to bird intruders or a general response to any form of nest disturbance.

A Sony video camera (CCD-TR 660E Hi 8) was mounted on a stand and placed at a distance of 3–4 m and levelled 0.4 m above the nests. The camera was powered with a 12-volt car battery and provided with a shelter painted dark green to be inconspicuous. Since all the nests were situated above water, the battery was placed on the shore and connected to the camera with a cable. Reed Warblers are known to be tolerant to human presence (Lindholm & Thomas 2000). They start to feed their broods almost immediately after cameras or hides are placed near their nests (latency to start of feeding for cameras = 5.00 ± 0.99 min (mean ± sd), n = 5; latency to start of feeding for hides = 3.08 ± 2.10 min, n = 13) and the age of brood does not influence this latency (r = –0.04, P = 0.90, n = 13; T. Grim, M. Honza, B. Matysioková & K. Voslajerová unpubl. data). Furthermore, feeding frequencies observed at the nest immediately after placing cameras or hides are the same as those reported by Kilner *et al.* (1999) who left cameras near the nest for several hours for birds to habituate. Thus, the effect of cameras on Reed Warbler behaviour is undetectable and it is highly unlikely that it could confound our results (moreover, we were interested in among-group differences and all groups were treated identically with cameras). Also the behaviour of the closely related Great Reed Warbler is not significantly affected by a video camera near the nest (M. Honza & C. Moskát, unpubl. data). Finally, responses of Reed Warblers towards a stuffed Cuckoo in the current study were almost the same as those in a previous study (Røskaft *et al.* 2002a) where host behaviour was directly observed without cameras. Nevertheless, we left the place for 1 hour allowing the birds to habituate to the set-up. After 1 hour, we presented the Cuckoo or stuffed Pigeon dummy mounted on a wooden pole 1 m from the nest. The dummies were in perching position and at the same height as the focal nest.

The behaviour of the nest owners was observed during a 5-min period from a distance of 10 m. We recorded latency time to arrival, latency time to alarm calling from the first arrival and time spent within 1 m of the Cuckoo/Pigeon dummy. The overall level of nest defence was rated on an ordinal scale: 0 = no response (no bird arrived during the 5-min period); 1 = silent watching; 2 = mobbing (i.e. flights around the dummy and alarm calls); 3 = contact attack(s); see Moksnes *et al.* (1990) for the description of these behaviours. All observations were made by one researcher (M.H.) to avoid possible observer bias.

After presentation of the dummy and clutch manipulation (see above), the dummy was removed and the camera was switched on. Nests were videotaped for 30 minutes. In the case of the human intruder group, we followed a similar pattern. The camera was set up 1 hour before an observer approached the nest. The observer stood near the nest for 2 min (almost all the pairs responded up to this time). After this period the camera was switched on and the observer left.

The videotapes were analysed in the laboratory. From the tapes we recorded the arrival time (time to first sight of the nest owner/s), brooding time (time from when the camera was switched on until the host started brooding), look-1 (time spent with nest inspection behaviour, from the moment when the bird first looked into the nest until the moment when it first sat on the clutch) and look-2 (total time spent inspecting the nest after the bird sat on it. Look-1 is not included in look-2. Nest inspection behaviour is defined as the bird looking at the clutch. The number of arrivals at the nest (this variable should reflect the amount of host activity at the nest) and nest time (total amount of time spent at the nest) were also recorded.

RESULTS

Nest defence and enemy recognition (prediction 1)

There were no statistically significant differences in any of the behavioural variables when Reed Warblers were facing Cuckoo or Pigeon dummies (Table 1). Absence of significant discrimination was not caused by absence of nest defence – some Reed Warblers responded with alarm calling; however, only two individuals attacked the Cuckoo dummy. Pigeons were never attacked. The difference in the number of experiments with attacks on Cuckoo and Pigeon dummies was, however, not significant (Fisher's exact probabilities test, ns).

Table 1. Responses of Reed Warblers to a Cuckoo dummy and a stuffed Pigeon. Values are medians (results of Mann–Whitney tests are shown). Nest defence: 0 = no response, 1 = silent watching, 2 = mobbing, 3 = contact attack (see Methods for further explanation).

Variable	Cuckoo (n = 41)	Pigeon (n = 16)	U	P
Latency to first response (min)	3.0	2.0	1.35	0.17
Latency to alarm calling after first response (min)	1.2	0.2	1.57	0.12
Time spent within 1m from the nest (s)	8.5	42.0	1.69	0.09
Median level of nest defence	1	1	1.56	0.12

Clutch inspection behaviour (prediction 2)

The experimental procedure had no significant effect on Reed Warbler's behaviour during the 30-min period immediately after the experiment (Kruskal–Wallis ANOVA tests, $P > 0.10$ in all cases; Table 2). After seeing the Cuckoo dummy at the nest, Reed Warblers did not tend to arrive at their nests significantly earlier, they did not spend significantly more time with nest inspection behaviour and their activity was not significantly different from those who saw the Pigeon dummy near their nests. The addition of a Cuckoo egg to the host nest had no effect on Reed Warbler behaviour. There was no significant difference in the way a human intruder affected host behaviour compared to dummies (Table 2).

Only six Reed Warbler pairs did not visit their nests during the 30-min period (two in Cuckoo – morning, two in Cuckoo – afternoon, one in Cuckoo + egg replacement – morning, one in Pigeon – afternoon). We observed no ejection or egg pecking of the Cuckoo egg during the 30-min observation period.

Effect of time of day on host behaviour (prediction 3)

Reed Warblers generally tended to spend slightly more

Table 2. Behaviour of Reed Warblers during the first 30-min period following the dummy experiments. Results are means ± sd. See Methods for explanations of the measured variables.

Variable	Cuckoo (n = 30)	Cuckoo + egg (n = 11)	Pigeon (n = 16)	Human (n = 14)	Kruskal–Wallis test (H)	P
Arrival time (s)	341 ± 369	379 ± 510	424 ± 507	170 ± 152	2.47	0.48
Brooding time (s)	353 ± 377	389 ± 508	388 ± 502	189 ± 156	1.98	0.57
Look-1 (s)	4.7 ± 5.5	10.4 ± 14.1	6.9 ± 8.0	4.4 ± 6.6	2.98	0.39
Look-2 (s)	9.9 ± 11.2	9.1 ± 3.8	5.5 ± 4.2	5.7 ± 6.0	5.45	0.14
No. of arrivals	2.5 ± 1.4	3.0 ± 1.9	2.1 ± 1.0	2.0 ± 0.7	1.59	0.66
Nest time (min)	18.5 ± 8.4	17.8 ± 10.4	18.5 ± 10.1	22.4 ± 6.5	2.96	0.41

time at the nest in the morning (70.4% of the observation time) than in the afternoon (56.9%), although the differences were not statistically significant (Table 3). Furthermore, we found no significant differences in clutch inspection behaviour by Reed Warblers between the morning and afternoon experimental groups (Table 3). Finally, the intensity of nest defence was almost identical between the morning and afternoon (Table 3).

Interestingly, host responses were highly variable among individuals. Individuals that quickly responded to the dummies also quickly arrived at their nests during the following 30-min period ($r_s = 0.404$, $n = 41$, $P = 0.009$). Furthermore, Reed Warblers who arrived at their nests quickly reacted more immediately with alarm calling, while those individuals arriving later in response to the dummy tended to delay their alarm calling response ($r_s = 0.955$, $n = 41$, $P < 0.001$).

DISCUSSION

Nest defence and enemy recognition (prediction 1)

Our prediction 1 of a more intense nest defence behaviour against the Cuckoo dummy than against the Pigeon dummy was not supported. In general, the level of nest defence by Reed Warblers in our study area was relatively low, only 4.9% of pairs attacked the Cuckoo dummy which is in accordance with previous findings of Røskaft *et al.* (2002a, 2002b). A low level of aggression provides potential for errors in enemy recognition which could explain why responses to the Cuckoo and Pigeon were not significantly different.

Absence of specific recognition of the Cuckoo could be explained by the fact that the Reed Warbler is an intermediate rejecter (rejection rate of natural Cuckoo eggs is 37.5% in our study areas; Øien *et al.* 1998) – egg rejection and aggression against adult parasites evolve in concert, i.e. acceptors are less aggressive than rejecters (Røskaft *et al.* 2002b). Thus, intermediate rejecters could be expected to show low levels of aggression and also poorer abilities to recognize adult parasites. Our results are in line with this general relationship between parasitic egg and adult parasite related adaptations. Low level of aggression and poor enemy recognition in the Reed Warbler are also expected from the spatial habitat structure hypothesis (Røskaft *et al.* 2002c) – species with some populations breeding in the vicinity of trees (Cuckoo observation points) and some breeding away from trees generally have lower egg rejection rates (Røskaft *et al.* 2002c) and less aggressive response to the parasite (Røskaft *et al.* 2002c) than species always breeding close to Cuckoo perches in trees. In the former (including Reed Warbler) there is lower selection pressure for anti-parasitic adaptations (including specific enemy recognition) than in the latter. Thus, our results (low aggression, poor enemy recognition) accord with the spatial habitat structure hypothesis.

Despite being regularly parasitized (Moksnes *et al.* 1993b, Øien *et al.* 1998) Reed Warblers in our study area behaved similarly to individuals from unparasitized populations in Britain (Lindholm & Thomas 2000; see also Røskaft *et al.* 2002). Duckworth (1991) found that Reed Warblers in his study area in England recognized

Table 3. Effect of time of day on Reed Warbler behaviour at their nests during the first 30-min period following the dummy experiment. The data presented are medians (results of Mann–Whitney tests are shown). Nest defence was rated on an ordinal scale (see Table 1). Sample sizes for morning/afternoon experiments are: Cuckoo 14/16, Cuckoo + egg 7/4, Pigeon 9/7, human 5/9.

Variable	Experimental procedure	Morning	Afternoon	*U*	*P*
Time spent at the nest (% of total observation)	Cuckoo	70.8	54.5	1.15	0.25
	Cuckoo + egg	72.3	40.2	0.96	0.34
	Pigeon	66.7	56.5	0.89	0.37
	Human	71.7	76.4	0.33	0.74
	Mean	70.4	56.9	1.29	0.20
Nest inspection = Look-1 (s)	Cuckoo	2.5	2.0	0.21	0.83
	Cuckoo + egg	3.0	7.0	0.54	0.59
	Pigeon	4.5	3.0	0.93	0.35
	Human	1.0	3.0	0.82	0.41
	Mean	3.0	3.0	0.24	0.81
Nest defence (0–3)	Cuckoo	1.5	1	0.55	0.58
	Cuckoo + egg	2	1	0.93	0.35
	Pigeon	1	1	0.00	1.00
	Human	–	–	–	–
	Total	1	1	0.58	0.56

the Cuckoo as a special enemy while our results did not support the hypothesis. However, caution is needed in this comparison because the authors of the two studies did not follow the same experimental procedure – we presented dummies 1 m from the focal nest while Duckworth (1991) placed dummies at two distances, either directly at the nest or 3 m from the nest. He found that Reed Warblers responded much more aggressively to the dummy on the nest compared to one 3 m from the nest (see also Røskaft *et al.* 2002). More importantly, Duckworth (1991) observed significant differences in Reed Warbler responses towards different mounts only when dummies were placed directly at the nest – there were no significant differences when dummies were placed 3 m from focal nests.

Nest inspection behaviour (prediction 2)

We predicted that the host would show higher nest inspection activity after being exposed to a Cuckoo dummy than to a Pigeon dummy. We obtained no support for this prediction because Reed Warblers did not modify their behaviour in respect to the kind of intruder (Cuckoo, Pigeon or human). Including a Cuckoo egg in the nest in addition to the Cuckoo dummy did not influence the host behaviour. This could indicate that the sight of the Cuckoo at the nest was not a strong enough cue to indicate parasitism and thus release defence behaviour immediately after the act of parasitism. Moksnes *et al.* (1993a) have reported similar results for Meadow Pipit *Anthus pratensis* where the presence or absence of Cuckoo female and/or egg dummies had no significant effect on incubation and nest checking behaviours.

An explanation may be that the Reed Warbler needs time to discover parasitism. Like many other species it usually rejects parasitic eggs several days after being parasitized (Davies & Brooke 1988, Moksnes *et al.* 1990, Grim & Honza 2001, Amundsen *et al.* 2002). On the other hand the Meadow Pipit, another frequently used Cuckoo host which also is an intermediate rejecter, deserts its nest very quickly (sometimes within a few minutes after the act of parasitism) and always within 24 h after experimental manipulation (Moksnes *et al.* 1993a). However, even in this quickly rejecting species there were no differences in the behaviour of individuals who could see a Cuckoo dummy at their nests and those who could not (Moksnes *et al.* 1993a).

Davies & Brooke (1988) showed that a Cuckoo mount increases the probability that the Reed Warbler will reject the parasitic egg. Our observations indicate that this effect is not detectable immediately after the parasitism act.

Why the Cuckoo lays in the afternoon (prediction 3)

Reed Warblers did not spend more time at their nests in the morning compared with the afternoon, which gives no support for prediction 3. Davies & Brooke (1988) measured the temperature of Reed Warbler eggs in the morning and in the evening and found morning broods to be significantly warmer and concluded that Reed Warblers spent more time at their nests in the morning. However, our observations are in accordance with those obtained by Moksnes *et al.* (2000) who found no difference between the length of time that Reed Warblers spent at their nests in the forenoon and afternoon. Therefore, the absence of changes in nest attentiveness during the day does not support the view that Cuckoo afternoon laying has evolved because the host is away from its nest more during this part of the day.

Cuckoo afternoon laying could also result from a higher intensity of clutch inspection behaviour and nest defence by hosts in the morning. Our study does not support either of these behaviours because Reed Warblers showed no differences in clutch inspection and nest defence behaviours during the day.

Absence of immediate ejections

We did not observe any pecking or ejections during the 30-min period after we added a parasitic egg to a focal nest. We used natural Cuckoo eggs which in our study area do not correspond very well to Reed Warbler eggs as judged by the human eye (Edvardsen *et al.* 2001). However, Reed Warblers in our study area accept 62.5% of these natural parasitic eggs (Øien *et al.* 1998) and even highly non-mimetic eggs are frequently accepted (43.7%; Stokke *et al.* 1999).

Low aggression and absence of specific responses to the Cuckoo both during dummy experiments and in the 30-min period thereafter could result from the fact that the arms-race between the Cuckoo and *Acrocephalus* warblers in our study area is at a relatively early stage as indicated by host acceptance of badly matching Cuckoo eggs and a low match between parasitic and host eggs (Edvardsen *et al.* 2001). Honza *et al.* (2001) hypothesized that the fact that 86.3% of Cuckoo eggs laid in Reed Warbler nests belong to the *Sylvia* egg morph could be indicative of host switching due to construction of fish ponds in Moravia in the

16th century. The low level of host defences in our study area could represent an example of evolutionary lag. Alternatively, this finding could be explained by gene flow between parasitized and unparasitized populations, see Røskaft *et al.* (2002).

To explain poor Reed Warbler antiparasitic defences in our study area it is helpful to consider other sympatric hosts. The Great Reed Warbler is currently parasitized more frequently than the Reed Warbler (Kleven *et al.* 1999). Some 30 years ago Reed Warbler and Great Reed Warbler were equally common (Hudec 1975). At present the Great Reed Warbler is almost absent from the study area (but is still preferred as a host). If in the past Cuckoos also laid their eggs preferentially in the nests of the Great Reed Warbler then it is possible that the selection for specific host adaptations in the Reed Warbler was weak before the recent decline of the Great Reed Warbler in the study area.

In conclusion, low level and specificity of host responses after presentation of stuffed dummies in our study area could be expected from the fact that the Reed Warbler is an intermediate rejecter of Cuckoo eggs (Røskaft *et al.* 2002b). This could result from a relatively short co-evolution between host and parasite (see also Edvardsen *et al.* 2001, Honza *et al.* 2001) and is in line with the spatial habitat structure hypothesis (Røskaft *et al.* 2002c).

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