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## HOST RECOGNITION OF BROOD PARASITES: IMPLICATIONS FOR METHODOLOGY IN STUDIES OF ENEMY RECOGNITION

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**ABSTRACT.**—Various studies have shown that experiments on nest defense and enemy recognition (e.g. recognition of adult brood parasites) can be confounded by many factors. However, no study has described a confounding effect of control dummy type. Here, I show experimentally that the choice of control dummy may influence the results of an experiment and lead to erroneous conclusions. I tested recognition abilities of the Blackcap (*Sylvia atricapilla*), currently a host rarely used by the Common Cuckoo (*Cuculus canorus*). Blackcaps responded very differently to two kinds of control dummies: they ignored the Eurasian Blackbird (*Turdus merula*) dummy, but attacked the Rock Pigeon (*Columba livia*) dummy as frequently as they attacked the Common Cuckoo. The differing results may be explained by the fact that the Rock Pigeon is more similar to the Common Cuckoo than the Eurasian Blackbird is, and consequently elicited more aggressive behavior than the latter. Thus, absence of discrimination in enemy-recognition studies may reflect a methodological artifact resulting from varying abilities of particular hosts to discriminate along a continuum of recognition cues. This result has serious methodological implications for further research on enemy recognition and aggression in general: a control dummy should not be too similar to the dummy brood parasite; otherwise, the chance of detecting existing recognition abilities is low. Further, I argue that coevolution only increases pre-existing aggression in the particular host species. Therefore, increment analysis (assessing changes in host antiparasitic responses during the nesting cycle while controlling for background aggression to control dummies) provides a more accurate picture of hosts' recognition abilities than the traditional approach (when the total level of antiparasitic response is analyzed). Received 30 January 2004, accepted 3 November 2004.

**Key words:** brood parasitism, coevolution, discrimination, methodology, nest defense, recognition.

### Reconocimiento del Hospedero de los Parásitos de Nidada: Consecuencias para las Metodologías de Estudios sobre Reconocimiento del Enemigo

**RESUMEN.**—Varios estudios han mostrado que los experimentos sobre defensa de nidos y reconocimiento del enemigo (e.g. reconocimiento de parásitos de nidadas adultos) pueden ser equívocos por muchos factores. Sin embargo, ningún estudio ha descrito un efecto equívoco dado por el tipo de modelo usado como control. En este estudio, demuestro experimentalmente que la elección del modelo puede influenciar los resultados de un experimento, conduciendo a una conclusión errónea. Probé las habilidades de reconocimiento de *Sylvia atricapilla*, que es actualmente un hospedero raramente usado por *Cuculus canorus*. *S. atricapilla* respondió de manera muy diferente ante dos tipos de modelos control: ignoraron a modelos de *Turdus merula*, pero atacaron a modelos de *Columba livia* tan frecuentemente como atacaron a *C.*

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*canorus*. Las respuestas diferenciales pueden ser explicadas por el hecho que *C. livia* es más similar a *C. canorus* que a *T. merula*, por lo que provocó un comportamiento más agresivo que contra *T. merula*. Por lo tanto, la falta de discriminación en estudios sobre el reconocimiento de enemigos puede estar reflejando un artefacto metodológico que resulta de la variación en la habilidad de un hospedero en particular de discriminar a lo largo de un continuo de señales de reconocimiento. Este resultado presenta serias consecuencias metodológicas para estudios futuros sobre reconocimiento de enemigos y sobre agresividad en general: el modelo utilizado como control no debe ser muy parecido al modelo del parásito de nidada; de lo contrario, la probabilidad de detectar la habilidad de reconocimiento existente es muy baja. Además, argumento que la coevolución sólo aumenta la agresión preexistente en una especie hospedera en particular. Por lo tanto, los análisis de incremento (la determinación de los cambios en las respuestas antiparasitarias de los hospederos durante el ciclo de nidificación mientras se controla por la agresión de fondo hacia modelos control) brindan una mejor idea sobre las habilidades de reconocimiento de los hospederos que el enfoque tradicional (cuando el nivel total de la respuesta antiparasitaria es analizado).

ALL ANIMALS ARE subject to strong selection pressure from various environmental factors, including predators (Montgomerie and Weatherhead 1988) and brood parasites (Rothstein and Robinson 1998). Response or absence of response to those stimuli may have an important effect on an individual's fitness. Given that brood parasites may reduce host reproductive success (Rothstein 1990), the best defense against parasitism should be to deter a parasitic female from laying her egg in a host nest in the first place (Sealy et al. 1998). However, nest defense, like any other activity around the nest, can be costly—it can attract predators (Martin et al. 2000) or brood parasites (Banks and Martin 2001), there may be a trade-off with parental care (Ueta 1999), and the defending parent risks injury (McLean et al. 1986, McLean 1987, Montgomerie and Weatherhead 1988). Selection, then, should favor recognition of specific intruders. Importantly, the difference between the generalized nest defense and a specific response to the parasite is not relevant, *per se*, to host avoidance by the parasite—both responses could reduce the probability of parasitism. However, specific enemy recognition can be important evidence of host-parasite coevolution (Sealy et al. 1998).

Host ability to recognize the parasite as a unique enemy and to respond aggressively has been studied in various hosts of the Brown-headed Cowbird (*Molothrus ater*; e.g. Robertson and Norman 1976, 1977; Briskie and Sealy 1989; Burgham and Picman 1989; Hobson and Sealy

1989; Neudorf and Sealy 1992; Gill and Sealy 1996, 2004; Gill et al. 1997a, b; Sealy et al. 1998). By contrast, relatively less is known about the enemy-recognition capabilities of host species parasitized by the Common Cuckoo (*Cuculus canorus*; hereafter "cuckoo"). The cuckoo hosts that have been properly tested for specific enemy recognition include only the Reed Warbler (*Acrocephalus scirpaceus*; Duckworth 1991, Lindholm and Thomas 2000, Honza et al. 2004), Great Reed Warbler (*A. arundinaceus*; Bartol et al. 2002), Meadow Pipit (*Anthus pratensis*; Moksnes and Røskaft 1989), Eurasian Blackbird (*Turdus merula*), and Song Thrush (*T. philomelos*) (Grim and Honza 2001). Other authors have studied responses of cuckoo hosts toward the parasite (e.g. Smith and Hosking 1955, Moksnes and Røskaft 1988, Moksnes et al. 1990, Røskaft et al. 2002). They found that species that are appropriate hosts and have probably been involved in a coevolutionary "arms race" with the cuckoo were significantly more aggressive toward the parasite than species that were not appropriate hosts (i.e. hole nesters, seed eaters).

However, even unsuitable hosts showed some aggression toward cuckoos (e.g. Røskaft et al. 2002). Thus, it is possible that some species are aggressive against any intruders near the nest, including innocuous ones (Bazin and Sealy 1993). Although the results of the above studies are suggestive, their conclusions would clearly be stronger if experiments where host responses to both parasite and nonthreatening

controls were compared (for detailed discussion, see Sealy et al. 1998).

In general, it is important to differentiate between a generalized nest defense (i.e. host responds to various intruders—parasite, predator, food competitor, nest-site competitor, even innocuous species—with similarly aggressive responses) and a specific response to the parasite (i.e. host ignores nonthreatening intruders or shows significantly lower response to them than to the parasite at an early stage in the nesting cycle, when parasitism is a greater threat). Only the latter could be accepted as evidence of coevolution between the parasite and a particular host (Neudorf and Sealy 1992, Gill and Sealy 1996, Sealy et al. 1998). Moreover, all European species tested for specific recognition so far are either acceptors or current common hosts that reject only at intermediate frequencies (Moksnes and Røskaft 1989, Duckworth 1991, Lindholm and Thomas 2000, Grim and Honza 2001, Bártol et al. 2002). Virtually nothing is known about enemy-recognition abilities of strong egg-rejecters parasitized by the cuckoo.

Further, from the point of view of studies of nest defense and recognition in general, it is crucial to understand factors that could confound the results of such studies. A wide array of confounding factors has received attention (e.g. number of previous visits to a tested nest, posture of the experimental intruder, live vs. mounted predator, etc.; Knight and Temple 1986a, b; for reviews, see Montgomerie and Weatherhead 1988, Sealy et al. 1998). However, the possible confounding effect of the type of control dummy used has not been properly examined before. Although Robertson and Norman (1976, 1977) used various control dummies, they reported that responses to different control dummies were the same and lumped the results without providing details. Given that no recognition system can be perfect, every individual will commit recognition errors if presented with two stimuli that are sufficiently similar (Sherman et al. 1997). Hosts of parasitic birds vary in their discrimination capabilities—toward both eggs (e.g. Davies and Brooke 1989) and adult parasites (e.g. Sealy et al. 1998). Therefore, we can reasonably expect that tested individuals of less-discriminating host species will respond aggressively even to innocuous intruders if they are too similar to really threatening intruders. That could lead to confusion in the interpretation of results of enemy-recognition studies.

I studied enemy recognition and nest-defense behavior of the Blackcap (*Sylvia atricapilla*), a suitable host for the cuckoo (Moksnes and Røskaft 1995). Analysis of museum-held clutches of European passerines indicated that the Blackcap was the 16th most frequent cuckoo host in Europe (Moksnes and Røskaft 1995). Furthermore, Blackcaps are strong rejecters of both nonmimetic (76.9%; Moksnes et al. 1990) and mimetic (100.0%; Moksnes and Røskaft 1992) eggs introduced into their nests, which indicates that Blackcaps have been frequently parasitized by the cuckoo in their evolutionary history. However, there are no recent reports of cuckoo parasitism on Blackcaps. Moksnes et al. (1990) and Røskaft et al. (2002) recorded high levels of aggression by Blackcaps toward the cuckoo dummy; however, they did not use a control.

Therefore, I investigated specific enemy recognition in the Blackcap, testing two hypotheses: (1) the generalized nest-defense hypothesis, which suggests that hosts do not recognize a brood parasite as a unique enemy and predicts similar response to parasites and innocuous controls; and (2) the specialized nest-defense hypothesis, which assumes that hosts recognize the parasite as a unique threat and predicts that hosts show aggression only (or more so) to parasites but ignore (or show significantly lower response) to controls. Additionally, I used two control dummies that differed in the degree to which they resembled the cuckoo to examine whether the choice of control dummy type may confound the ability of researchers to distinguish between those two hypotheses.

#### METHODS

*Study site and species.*—I conducted the study in a deciduous forest near the village of Dolní Bojanovice (48°52'N, 17°00'E), in the southeastern Czech Republic, ~60 km southeast of Brno. Data were collected from 25 April to 30 June in 2000 and 2001. Because the data were not significantly different between years (and data analyzed separately for the each field season gave qualitatively the same results), I pooled the data.

Nest defense was tested with stuffed (taxidermic) dummies. I primarily followed the experimental procedure suggested by Sealy et al. (1998); however, I did not use a predator

dummy, for reasons elaborated below. I tested host responses toward the cuckoo (the brood parasite), the Rock Pigeon (*Columba livia domestica*; hereafter "pigeon"; control 1) and the Eurasian Blackbird (adult male; hereafter "blackbird"; control 2). I used two stuffed cuckoo dummies in experiments (responses to each were identical).

The pigeon dummy was pale gray (a shade similar to the cuckoo's) overall, with two dark wing bars and a dirty white rump. The pigeon and cuckoo dummies were almost the same size (measured from the base of the bill to the wing tip: pigeon 25.0 cm, cuckoo 25.5 cm), though the cuckoo had a longer tail (17 cm) than the pigeon (12 cm). The blackbird dummy was a bit smaller (23 cm; tail 10 cm), overall black with yellow bill and eye ring. The cuckoo also had a yellow bill and eye ring.

The pigeon and blackbird were chosen as controls because both are completely innocuous for the Blackcap: they are neither brood parasites nor predators, and there is no confounding effect of competition for food and nest sites. Some researchers prefer to use control species that are familiar to tested hosts (e.g. McLean 1987, Moksnes and Røskaft 1989), whereas others argue it is better to use controls that do not occur on the study area (e.g. Hobson and Sealy 1989). I believe that a control species that is familiar to a tested host species provides a stronger test for enemy-recognition abilities because hosts have had prior opportunities to compare the threatening and nonthreatening sympatric species and adapt their behavior correspondingly (see also Mark and Stutchbury 1994). Either way, Sealy et al. (1998) suggested that prior (in)experience with a control species should have no effect. Blackcaps, blackbirds, pigeons, and cuckoos occur in sympatry in my study area.

*Experimental procedure.*—I performed two series of paired experiments during the laying stage, when the cuckoo represents the greatest danger to the host (Davies and Brooke 1989). In the first series ( $n = 20$  nests), I tested responses to the cuckoo and pigeon; in the second ( $n = 15$  nests), to the cuckoo and blackbird. These sample sizes are higher than sample sizes in several studies that observed significant differences in behavior to various intruders (e.g. Robertson and Norman 1976, 1977; Smith et al. 1984; McLean 1987; Hobson and Sealy 1989;

Duckworth 1991), and thus should be sufficient to test for specific recognition (for more details, see below). Because cuckoos are a threat to hosts also during incubation and nestling stages (when they depredate both eggs and nestlings at nests too advanced for successful parasitism; e.g. Jourdain 1925, Gärtner 1981), I also tested host responses to the cuckoo and pigeon dummies during incubation ( $n = 20$ ) and nestling ( $n = 20$ ) stages. Blackcaps start to incubate with the penultimate egg (Cramp 1992), and some nests were tested on a day when the penultimate or last egg was laid. Those nests are included in the "laying stage" group.

Models were presented at random to eliminate order effects (Kamil 1988). First, I attached one of the dummies in a life-like position to a branch ~0.5 m from each nest, level with it and facing the nest rim. Timing started after I retreated to the blind, set  $\geq 15$  m from the nest. After one parent appeared near the nest and became aware of the dummy, I observed reactions of nest owners for 5 min (from the moment the first parent arrived, even when it did not respond aggressively to the dummy). Presentation of the second mount at the same place was separated by 30 min to avoid habituation or carry-over aggression (Sealy et al. 1998).

Each nest was tested only once to avoid pseudoreplication. In 2000, almost all Blackcaps breeding in the forest were ringed (M. Honza, V. Mrlík, M. Čapek, P. Procházka unpubl. data). In 2001, I observed only one ringed bird among tested individuals; therefore, probably no particular bird was tested in both years.

Intensity of Blackcap responses varied from quiet watching at a short distance to vigorous attacks (i.e. flying at and hitting the dummy; close passes are not included in attacks; see below). Because the frequency of alarm calling ("Tak-calls"; Cramp 1992), attacks, and so forth was too high to be recorded exactly on the data-sheet, but discrete categories of host behavior (see below) were clearly definable, I categorized behaviors according to relative scales (see also McLean et al. 1986, Pavel and Bureš 2001). Both male and female responses were combined for each of the defense categories if both parents were present. I scored the frequency of alarm calling (0 to 3; 0 = no vocalizations, 1 = overall time spent calling <1 min, 2 = calling <3 min, 3 = calling >3 min) and attacks (i.e. bird contacted dummy; 0 to 2; 0 = no attacks, 1 = <5 attacks,

2 = >5 attacks). Total level of nest defense was ranked on a scale depending on the risk taken by tested bird(s) (0 to 4; 0 = no response, i.e. silent watching of dummy; 1 = few vocalizations, bird[s] >5 m from dummy; 2 = more vocalizations, bird[s] <5 m from dummy; 3 = frequent vocalizations and close passes; 4 = frequent vocalizations and attacks). Total level of nest defense is the overall effort of nest owners (both male and female) defending the nest. I also recorded delay in arrival of nest owner(s) (in minutes), number of individuals that responded, and time spent <1 m from the dummy (in minutes).

*Data analyses.*—I analyzed data in three ways (see also Maloney and McLean 1995). First, I compared differences in responses to dummies using five variables probably related to quality of nest defense (latency to response, frequency of alarm calling, time spent <1 m from a dummy, frequency of attacks, and number of individuals performing nest defense) to make different aspects of host behavior comparable with other studies (see Sealy et al. 1998). The five variables describe all behaviors Blackcaps performed when confronted with dummies (no Blackcaps fluttered or dived above the dummy, as other species do, e.g. Collared Flycatchers [*Ficedula albicollis*]; T. Grim unpubl. data). Second, I tested for differences between responses to dummies in Blackcaps' total level of nest defense (see above). Third, because the different measures of nest defense were intercorrelated, I performed principal components analysis (PCA) on alarm calling, attacks, and number of individuals responding (I included the latter factor because it theoretically could have an important effect on probability of deterring the cuckoo from the nest; I did not include latency and time spent <1 m from a dummy, for reasons given below).

Because the responses were measured on an ordinal scale (see above), I analyzed data by nonparametric Wilcoxon signed-ranks tests and Mann-Whitney *U*-tests. To keep the experiment-wise error rate at  $\alpha = 0.05$ , I used Bonferroni correction.

## RESULTS

### CONFOUNDING VARIABLES

Avian nest defense can be influenced by various factors (Montgomerie and Weatherhead

1988). Thus, before statistically testing for recognition abilities in Blackcaps, I checked whether the level of nest defense was influenced by the reproductive value of the nest (calculated as a product of clutch or brood size and age of the clutch or brood), time of season, time of day, number of previous visits to the nest, and nest concealment. I found no significant effect of those confounding variables (T. Grim unpubl. data). Moreover, all those variables were held constant because of the within-subject design (Kamil 1988) of the study.

Results of PCA on alarm calling, attacks, and number of individuals showed that the first principal component (PC1) explained 59.7% of variance in the data. The first principal component was positively correlated with the remaining three nest-defense variables (alarm calling:  $r_s = 0.77$ ,  $P = 0.001$ ; attacks:  $r_s = 0.73$ ,  $P = 0.001$ ; number of individuals:  $r_s = 0.79$ ,  $P = 0.001$ ). Intensity of nest defense (PC1) did not change during the nesting cycle, from laying to nestling stages (responses to cuckoo: Kruskal-Wallis ANOVA,  $\chi^2 = 0.34$ ,  $df = 2$ ,  $P = 0.84$ ; responses to pigeon:  $\chi^2 = 2.09$ ,  $df = 2$ ,  $P = 0.35$ ; the same result was obtained for total level of nest defense on the ordinal scale). Given that coevolution between a parasite and host may only increase pre-existing general aggression (see below), I controlled for possible variation in general ("background") nest defense during the nesting cycle by subtracting intensity of aggression toward the control (pigeon) from intensity of aggression to the parasite (cuckoo). That stronger test confirmed that there is no relationship between anti-cuckoo aggression and nesting cycle (Kruskal-Wallis ANOVA,  $\chi^2 = 0.13$ ,  $df = 2$ ,  $P = 0.94$ ).

Recognition abilities can be age-dependent (Smith et al. 1984). Older birds breed earlier (Sæther 1990) and can show better enemy recognition (Smith et al. 1984) or stronger nest defense (Hobson and Sealy 1989), which could have confounded the results. However, logistic regression showed no effect of time of season (date of the first egg laid) on distribution of birds responding "correctly" (more response to cuckoo) and "incorrectly" (same response to the two dummies, stronger response to pigeon, or no response to either dummy;  $r^2 = 0.02$ ,  $\chi^2 = 1.23$ ,  $df = 1$ ,  $P = 0.27$ ,  $n = 60$ ).

Order of presentation of dummies had no effect on any variables included in comparisons when data from first and second presentations

of the cuckoo dummy were compared (Mann-Whitney *U*-tests: all nonsignificant). The same result was obtained from comparison of first and second presentations of pigeon and blackbird dummies and when data for incubation or incubation and nestling periods were included. There were no differences in response to first and second dummy (Wilcoxon matched-pairs tests: all nonsignificant). Thus, there was no confounding effect of habituation.

CUCKOO-PIGEON EXPERIMENTS

Responses toward the cuckoo and pigeon dummies were very similar in all three nesting stages (Table 1). Blackcaps approaching both types of dummies typically uttered alarm calls (“*Tak*-calls”) at a very high frequency (~30 per 10 s; T. Grim pers. obs.; see also sonogram in Cramp 1992). Both the cuckoo and pigeon dummies were frequently attacked (proportion of experiments when a dummy was attacked at least once; laying stage: cuckoo: 42.9%, pigeon: 35.0%:  $\chi^2 = 0.33$ , *df* = 1, *P* = 0.57; all stages pooled:

cuckoo 38.3%, pigeon 28.3%:  $\chi^2 = 1.35$ , *df* = 1, *P* = 0.24). There were no significant differences between dummies in the frequency with which alarm calling and attacks were elicited from the Blackcaps (Table 1). The result was consistent among three types of analyses of data (Table 1).

CUCKOO-BLACKBIRD EXPERIMENTS

Blackcap responses to the cuckoo and innocuous pigeon were not significantly different, despite the large sample size (*n* = 60) when data for all nesting stages were pooled. Therefore, I tested for responses to the cuckoo and another control dummy—the blackbird—in the second series of experiments. I found clear differences in host behavior (Table 2). Responses to the cuckoo were again aggressive (40% of experiments with an attack) and did not differ significantly from responses to cuckoos during laying stage in the first series of experiments (Mann-Whitney tests, all nonsignificant). In striking contrast, when confronted with the blackbird dummy, Blackcaps never uttered alarm calls,

TABLE 1. Summary of Blackcap responses to dummy cuckoo (C) and pigeon (P) during three nesting stages. In the far right column, data from all stages are pooled.

Response variable <sup>a</sup>	Dummy type	Egg laying ( <i>n</i> = 20)	Incubation ( <i>n</i> = 20)	Nestling ( <i>n</i> = 20)	All stages ( <i>n</i> = 60)
Latency (minutes)	C	10.1 ± 2.5	4.1 ± 0.7	5.6 ± 1.3	6.6 ± 1.0
	P	11.8 ± 2.6	4.6 ± 0.7	5.1 ± 1.3	7.2 ± 1.0
Alarm <sup>b</sup>	C	2	2	2	2
	P	2	2	2	2
Less than 1 m (minutes)	C	3.0 ± 0.4	2.5 ± 0.5	3.3 ± 0.5* <sup>f</sup>	2.9 ± 0.3* <sup>f</sup>
	P	3.0 ± 0.5	2.3 ± 0.5	2.9 ± 0.5	2.7 ± 0.3
Attacks <sup>c</sup>	C	0	0	0	0
	P	0	0	0	0
Number of individuals	C	1.3 ± 0.1	1.6 ± 0.1	1.7 ± 0.1	1.5 ± 0.1
	P	1.4 ± 0.1	1.7 ± 0.1	1.8 ± 0.1	1.6 ± 0.1
Total level <sup>d</sup>	C	3	2	3	3
	P	3	2	3	3
PC1 <sup>e</sup>	C	0.06 ± 0.34	0.2 ± 0.3	0.3 ± 0.3	0.2 ± 0.2
	P	-0.14 ± 0.26	0.0 ± 0.3	0.4 ± 0.3	0.1 ± 0.2

<sup>a</sup> Values for latency, time spent <1 m from a dummy, number of individuals, and PC1 are means ± SE; values for alarm, attacks, and total level are medians.

<sup>b</sup> Ordinal scale: 0 = no vocalizations, 1 = overall time spent calling <1 min, 2 = calling <3 min, 3 = calling >3 min.

<sup>c</sup> Ordinal scale: 0 = no attacks (i.e. no bird contacted dummy), 1 = <5 times, 2 = >5 times.

<sup>d</sup> Ordinal scale: 0 = no response (i.e. silent watching of dummy); 1 = few vocalizations, bird(s) >5 m from the dummy, 2 = more vocalizations, bird(s) <5 m from dummy; 3 = frequent vocalizations and close passes; 4 = frequent vocalizations and attacks.

<sup>e</sup> PCA performed on alarm calling, attacks, and number of individuals. For details, see text.

<sup>f</sup> Asterisks indicate results of Wilcoxon signed-ranks test between models; *P* < 0.05. Difference in “Less than 1 m” is not significant after Bonferroni correction.

TABLE 2. Differences in responses of Blackcaps to stuffed dummies. Comparisons of host behaviors in the paired experiment (cuckoo–blackbird;  $n = 15$ ) and unpaired experiment (pigeon–blackbird; ( $n = 20, 15$ ) are shown. For brief explanations of response variables, see Table 1; for details, see text.

Response	Cuckoo–blackbird <sup>a</sup>				Pigeon–blackbird <sup>b</sup>	
	Parasite	Control	<i>t</i>	<i>P</i>	<i>U</i>	<i>P</i>
Latency	11.1 ± 1.1	11.2 ± 1.5	0.68	0.50	1.15	0.25
Alarm	2	0	−3.97	0.0001* <sup>c</sup>	−4.24	0.0001*
Less than 1 m	3.2 ± 0.5	4.0 ± 0.3	2.50	0.013	1.32	0.19
Attacks	0	0	−2.65	0.008*	−2.49	0.01*
Number of individuals	1.7 ± 0.1	1.2 ± 0.1	−3.22	0.001*	0.94	0.35
Total level	3	0	−3.97	0.0001	−4.82	0.0001
PC1	0.41 ± 0.0	−1.50 ± 0.3	−4.45 ± 0.11	0.0001	−3.71	0.0002

<sup>a</sup> Results of Wilcoxon matched-pairs tests; *t*-values lower than zero indicate higher response toward the cuckoo.

<sup>b</sup> Results of Mann-Whitney tests. *U*-values lower than zero indicate higher response toward the pigeon.

<sup>c</sup> Asterisks indicate differences significant at  $P = 0.05$  after sequential Bonferroni test (for the first five variables).

never attacked the dummy, and frequently (46.7% of experiments;  $n = 15$ ) resumed incubation (latency to incubation =  $1.4 \pm 0.4$  min;  $n = 7$ ). Incubation behavior was never observed during the first series of experiments, even when tested birds were not aggressive toward either the cuckoo or pigeon dummies. When faced with the blackbird near their nests, three Blackcaps uttered weak squeaky sounds, but no individual uttered alarm calls.

Latency to response did not differ between the cuckoo and blackbird trials (Table 2). I hypothesize that this variable probably reflects general incubation and nest-attentiveness patterns of the host and has no relationship with nest defense. This is supported by (1) nonsignificant correlations between latency and all measures of host nest-defense behavior (Spearman rank correlations,  $n = 35$ ; all nonsignificant) and (2) the fact that the significant decline of latency with age of nest completely disappears when data from egg-laying period (before incubation starts) are excluded (linear regressions; whole nesting cycle:  $r^2 = 0.19$ ,  $F = 15.6$ ,  $df = 1$  and  $68$ ,  $P = 0.0002$ ; without egg-laying period:  $r^2 = 0.01$ ,  $F = 0.43$ ,  $df = 1$  and  $33$ ,  $P = 0.52$ ).

In the cuckoo–pigeon experiments, the time spent near a dummy positively correlated with aggression. By contrast, in the cuckoo–blackbird trials, time spent near the dummy was correlated with absence of aggression (an inevitable effect of incubation behavior—when incubating, Blackcaps were <1 m from the dummy). Because time spent near the dummy shows opposing relationships in two respective series of experiments, I did not include that variable

in the PCA, because it would confound results. The possible confounding effect was confirmed when I recalculated PCA for frequency of alarm calling, time spent <1 m from the dummy, frequency of attacks, and number of individuals responding; the difference in responses to cuckoo and blackbird dummies was not significant (Wilcoxon matched-pairs test:  $t = -1.64$ ,  $P = 0.10$ ,  $n = 15$ ). That result is clearly spurious, because the difference in responses could hardly be higher than that shown by Blackcaps toward the cuckoo as compared with the blackbird.

In summary, Blackcaps showed significantly lower response toward the blackbird dummy than toward the cuckoo dummy in all measured variables (except latency to response; see above). Three types of analyses of the data gave the same results (Table 2). Responses to the blackbird were also significantly different from reactions to the pigeon during the laying stage (Table 2).

## DISCUSSION

### SPECIALIZED OR GENERALIZED RESPONSE?

The two series of experiments lead to different interpretations. The cuckoo–pigeon experiment indicated that Blackcaps do not recognize the cuckoo as a special enemy (they attack the innocuous pigeon at the same level of aggression as they do the cuckoo). That result supports the hypothesis that host responses can be described as a generalized nest defense (hypothesis 2; see above; Sealy et al. 1998). Coevolution with the cuckoo (together with other forces, like predation) could contribute to the host's aggressive

behavior, but it did not lead to the evolution of a nest defense based on specific recognition of various intruders.

The cuckoo–blackbird experiment supported the alternative hypothesis (1) that the Blackcap is capable of recognizing the cuckoo. The Blackcaps behaved adaptively—they vigorously attacked the parasite, whereas they completely ignored the innocuous blackbird. Absence of conspicuous response toward non-threatening intruders is adaptive, because loud alarm calls could increase the conspicuousness of the nest to predators or other brood parasites and, in turn, negatively influence reproductive success of aggressive individual(s) (e.g. McLean et al. 1986, Martin et al. 2000). This second series of experiments shows that interpretation of a coevolutionary relationship between Blackcaps and cuckoos based on cuckoo–pigeon experiments was erroneous and is explainable as a methodological artifact (see below).

The nonsignificant difference in responses toward the cuckoo and pigeon in the laying stage is hardly explainable by low sample size ( $n = 20$ ), because (1) many studies revealed significant differences with similar or lower sample sizes (e.g. Robertson and Norman 1976, 1977; Knight and Temple 1986b; McLean 1987; Duckworth 1991; McLean and Maloney 1998); (2) cuckoo–blackbird experiments in the present study clearly show that even smaller sample size ( $n = 15$ ) is sufficient to reveal significant differences in Blackcaps behavior; and (3) inclusion of data from incubation and nestling periods gave qualitatively the same results in all analyses, despite the big sample size ( $n = 60$ ) for a nonparametric paired test (see above). This analysis (where data from all three nesting stages are pooled) makes good sense, because nest stage does not influence intensity of nest defense in the Blackcap (see above). The cuckoo is not only a parasite but also a predator of eggs and nestlings of small passerines (e.g. Jourdain 1925, Gärtner 1981). Thus, it would be adaptive for a host to attack and recognize the cuckoo in all stages of nesting.

#### ENEMY RECOGNITION

Nest defense coupled with enemy recognition is an important strategy for hosts to avoid brood parasitism, because other strategies (egg ejection, nest desertion) may be more costly (even successful ejectors lose one or more of

their own eggs because laying cuckoos remove them; Davies and Brooke 1989). Results of the present study support the hypothesis that this antiparasitic adaptation evolved in the Blackcap. Thus, Blackcaps recognize both parasitic eggs (Moksnes et al. 1990) and parasitic adults as special threats. However, that ability is limited, given that Blackcaps regularly attacked the pigeon dummy. The similar responses to the pigeon and cuckoo dummies might be understood in the light of the observation of Smith and Hosking (1955) that Willow Warblers (*Phylloscopus trochilus*) attacked a cuckoo dummy and a cuckoo head without a body. Both the pigeon and cuckoo dummies have plain gray heads; if the gray head is a stimulus for antiparasitic aggression in Blackcaps, those hosts could easily attack not only cuckoos but also any nonthreatening intruder with a gray head. On the other hand, the yellow eye ring and bill are probably not recognition cues for Blackcaps, given that blackbirds share those traits with cuckoos and are not attacked at all. These hypotheses require further investigation by manipulating potential recognition cues (see e.g. Gill et al. 1997b). Comparable data from Great Reed Warblers indicate that they show better recognition of cuckoos, given that they commit much fewer recognition errors during nest defense than Blackcaps. In 10% of experiments, Great Reed Warblers mobbed or attacked an innocuous Eurasian Collared-Dove (*Streptopelia decaocto*) control dummy (Bártol et al. 2002), whereas Blackcaps mobbed or attacked a nonthreatening pigeon mount in 90% of experiments. However, this comparison is only tentative, because the Eurasian Collared-Dove and pigeon resemble the cuckoo to different degrees (at least to human eyes).

To conclude that Blackcaps recognize cuckoos as a special enemy, it was necessary to use nonthreatening dummies as controls. However, almost all hosts of the cuckoo have been tested without appropriate controls (e.g. Moksnes et al. 1990, Moksnes and Røskaft 1988, Røskaft et al. 2002). Those studies provide important insights into host behavior; however, their results would have been strengthened by controlled experiments, given that some tested species may be aggressive toward brood parasites not because they co-evolved with them, but because they attack any intruder near their nests (that possibility is supported by the fact that even species

that could not have coevolved with cuckoos, because of inaccessible nests or inappropriate diet, sometimes attack them; Moksnes et al. 1990, Røskaft et al. 2002). Brood parasitism is not the only force selecting for aggression against intruders; the same pressure is provided by predators (Curio et al. 1985) and competitors for food (e.g. Robinson 1992) and nest sites (e.g. Garcia and Arroyo 2002). Thus, host aggression against the parasite dummy (without a control experiment) provides only weak support for the hypothesis that brood parasitism is a force selecting for evolution of nest defense.

Furthermore, some controlled studies found no differences in responses to parasite and control dummies for some species tested (e.g. Robertson and Norman 1976, 1977; Bazin and Sealy 1993; Grim and Honza 2001; Honza et al. 2004). However, the results of those studies, too, may not be conclusive—experiments with more-dissimilar control dummies (than those used in the above-mentioned papers) may show that even those hosts recognize brood parasites as special enemies, but only poorly.

#### COEVOLUTION WITH A PARASITE ONLY INCREASES PRE-EXISTING AGGRESSION: IMPLICATIONS FOR INTERPRETATION OF RESULTS

It is generally believed that because brood parasites pose the greatest threat to their hosts during the egg-laying period, responses to them should decrease in later stages of the nesting cycle if a host recognizes the parasite as a special enemy (e.g. Briskie and Sealy 1989, Hobson and Sealy 1989, Sealy et al. 1998). In his study of enemy recognition in Field Sparrows (*Spizella pusilla*), Burhans (2001) concluded that Field Sparrows probably do not recognize Brown-headed Cowbirds as a special enemy, because responses to them increased from incubation to nestling stage (though insignificantly). However, responses to a nonthreatening Fox Sparrow (*Passerella iliaca*) control increased between the two stages as well. More importantly, responses (frequency of alarm calling) to the control increased much more (+120%) than responses to Brown-headed Cowbirds (+20%). Thus, this re-analysis of Burhans' (2001) data shows that the overall responsiveness of Field Sparrows clearly increased between incubation and nesting stages, regardless of the type of dummy (parasite, predator, control; see table 1 in Burhans 2001).

Importantly, if a host attacks both a parasite and innocuous intruders at a similar rate, it cannot be claimed that attacks on the parasite are the result of coevolution. Coevolution can only increase pre-existing aggressiveness; thus, a host's response to a parasite is not equivalent to the overall level of aggression. Rather, it is only the difference in aggression toward the parasite as compared with the host's response to an innocuous enemy (this is analogous to the fact that the predation cost of begging is the increase in the rate of predation caused by begging, not the overall rate of predation; Haskell 1999). Therefore, the measured response to Brown-headed Cowbirds should be adjusted to the increase in general host responsiveness by subtracting the response to the Fox Sparrow control from the response to the Brown-headed Cowbird. After that adjustment, the results are the opposite of those reported by Burhans (2001): response to Brown-headed Cowbirds at incubation stage (70.3 alarms per 5 min) is actually higher than that at nestling stage (38.3 alarms per 5 min)—which suggests that Field Sparrows recognize the Brown-headed Cowbird as a special enemy (as also indicated by significant difference between responses to parasite and control dummies at incubation stage). In conclusion, if there was coevolution between Field Sparrows and Brown-headed Cowbirds, the result is not an overall response of the former to the latter, but only an "aggression increment" (i.e. the difference between aggressiveness to parasite and to nonthreatening intruder).

A possible exception, in which the incremental increase in aggressiveness cannot explain the differential behavior of hosts to parasites and predators, is found in the Yellow Warbler (*Dendroica petechia*). That species preferentially uses specific alarm calls and nest-protection behavior toward Brown-headed Cowbirds (Gill and Sealy 1996, Gill et al. 1997b), and populations allopatric with Brown-headed Cowbirds do not express those behaviors (Gill and Sealy 2004). However, in other studies, no specific antiparasitic behavior (different from antipredator behavior) has been reported.

#### WHY ARE THERE DIFFERENCES IN RESPONSES TO TWO TYPES OF CONTROL DUMMIES?

The discrimination threshold of any recognition system is set by a trade-off between

acceptance errors (e.g. attacks on pigeon) and rejection errors (e.g. no response to cuckoo; see e.g. Sherman et al. 1997). By recognition errors, I mean a nonadaptive response to any stimulus (e.g. attack on innocuous intruder or absence of attack on threatening intruder). Increasing similarity of tested and control stimuli inevitably leads to a higher rate of occurrence of recognition errors (e.g. mimetic parasitic eggs elicit higher frequency of acceptance errors than non-mimetic eggs; e.g. Davies and Brooke 1989). Similarly, the pigeon (which is more similar to the cuckoo than the blackbird is, with regard to overall coloration, size, and shape) elicited a high frequency of recognition errors, whereas the blackbird (which exhibits more cues for recognition) elicited no recognition errors. In general, animals discriminate according to degree of resemblance between stimuli (i.e. there is a continuum of discrimination abilities along the continuum of resemblances; e.g. Rothstein 1982, Dittrich et al. 1993, Caley and Schluter 2003). Anecdotal observations (e.g. cuckoo attacking a wild pigeon, probably mistaking it for a territorial conspecific intruder; Radford 1991) indicate that birds commit similar kinds of recognition errors under natural conditions.

It is important to stress that the blackbird test is a stronger test of recognition abilities than the pigeon test, because the blackbird is less similar to the cuckoo than the pigeon is. Similarly, absence of rejection of conspecific eggs is not evidence of absence of egg recognition in a particular species (Moksnes and Røskaft 1992). A test with nonmimetic eggs provides much more reliable results; if a host does not reject even highly nonmimetic eggs, we can safely conclude that it has no recognition ability; if a host does not reject mimetic eggs, no firm conclusions can be drawn. On the other hand, tests with mimetic eggs can provide additional information on the quality (degree) of recognition. The same holds true for adult-parasite dummy experiments (see also Kamil 1988).

To explain the existence of any behavior, the costs and benefits associated with it need to be understood. For example, acceptance of parasitic eggs could be explained by low parasitism rate, or high costs of rejection, or both (Davies et al. 1996). To understand why Blackcaps recognized some intruders (e.g. blackbird) but not others (e.g. pigeon), we would have to obtain information on costs and benefits associated with their

responses, the probabilities of encounters with different intruders, and the effectiveness of deterring dangerous enemies from host nests. A complicating factor is that even unsuccessful aggression against a parasite could have benefits—if birds “know” they were parasitized, they tend to reject parasite eggs more frequently (Davies and Brooke 1989, Moksnes and Røskaft 1989). Therefore, the effectiveness of nest defense behavior is generally hard to establish (Sealy et al. 1998). However, both mathematical models and direct measurements of breeding success of hosts showing various levels of nest defense and enemy recognition would shed more light on the issue.

#### PREDATOR AS CONTROL DUMMY: DIFFERENT USEFULNESS OF COWBIRD VERSUS CUCKOO STUDIES?

Some authors have compared host responses to a brood parasite and a predator (e.g. Burgham and Picman 1989, Duckworth 1991, Neudorf and Sealy 1992, Soler et al. 1999). Theory predicts that responses to predators should increase during the nesting cycle (as the value of host progeny increases), whereas responses to parasites should decrease, because they pose the most threat during the early laying stage (Sealy et al. 1998). However, the observation that host responses to a parasite and predator are the same (e.g. Burhans 2001) may not necessarily mean that a host does not recognize a parasite as a specific threat. On one hand, one host species—Yellow Warbler—was reported to show a unique response (specific alarm calls and nest-protection behavior) that apparently evolved in response to brood parasitism and not nest predation (Gill and Sealy 1996, 2004). On the other hand, there is no reason to expect that hosts have to evolve some novel antiparasitic behavior—why not use old and well-established antipredator behaviors (see discussion of the evolution of novel antiparasitic responses vs. strengthening of pre-existing anti-intruder adaptations in Hosoi and Rothstein [2000])? Recognition of a parasite may merely be manifested in different patterns of nest defense against parasites than against predators during a nesting cycle (Neudorf and Sealy 1992). However, brood parasites also prey on host nestlings (Rothstein and Robinson 1998), which makes antiparasitic aggression adaptive throughout the nesting period. That effect is

probably more important in cuckoos, which are clearly predators of both eggs and nestlings (e.g. Jourdain 1925, Gärtner 1981), than in Brown-headed Cowbirds, which only sometimes prey on nestlings (see McLaren and Sealy 2000 and references therein). Thus, lack of difference in responses to parasite and predator would not provide unambiguous positive evidence for absence of recognition in a cuckoo host (e.g. Blackcaps attack cuckoos throughout the nesting period at the same level; see above; see also Briskie and Sealy 1989, Neudorf and Sealy 1992). However, it may provide the key test in Brown-headed Cowbird hosts (Sealy et al. 1998). In other words, use of a predator mount may be informative in experiments with hosts of some parasites (e.g. Brown-headed Cowbirds), but less so in experiments with others (e.g. cuckoos). Therefore, use of innocuous species as a control should generally provide a stronger test of host enemy-recognition abilities than use of a predator mount. However, it should be noted that the actual magnitude of host-nest predation by cuckoos as compared with Brown-headed Cowbirds is not well known at present.

#### CONCLUSIONS

The results of the present study indicate that (1) absence of discrimination in enemy-recognition studies may reflect a methodological artifact, (2) the narrow similarity of tested and control stimuli can lead to erroneous inferences about coevolution, (3) biased results might not be avoided even by using a control, (4) inclusion of some behavioral variables into a composite measure of nest defense (PCA) can confound results, (5) the Blackcap as an effective egg rejecter is highly aggressive toward the brood parasite, and (6) the Blackcap recognizes the parasitic cuckoo as a special enemy. Further, I suggest that the use of the predator dummy is important in experiments with Brown-headed Cowbird hosts (see Sealy et al. 1998) but may be less informative with cuckoo hosts because of possible differences in patterns of predation by the two brood parasites on hosts nests during the nesting cycle. Finally, coevolution only increases pre-existing aggression of the particular host species. Therefore, the increment analysis (testing for changes in host responses to parasites during the nesting cycle while controlling for background aggression toward control dummy) provides a better test

of host recognition abilities than the traditional approach (when the total level of antiparasitic response is analyzed and the confounding effect of background aggression is not controlled). This sort of approach is well established in other areas of research—for example, in controlling for background nest desertion in egg rejection experiments (e.g. Grim and Honza 2001, Lahti and Lahti 2002) or controlling for background predation in studies of cost of begging (Haskell 1999). Study of background aggression requires a standard experimental approach across study species. Background aggression should also be taken into account in comparative studies of host aggression (e.g. Røskaft et al. 2002), because validity of their results is based on an unproved assumption that background aggression does not differ among species.

The finding that an absence of discrimination may be a methodological artifact has important implications to future studies of enemy recognition. In cases where researchers find no significant differences in responses to tested and control stimuli, it would be useful to employ another control that is less similar to a brood parasite. That suggestion accords with a general rule that researchers should spread out the levels of the independent variable (e.g. a type of enemy dummy), so that effects are detected if they exist (Kamil 1988). Additional experiments can later focus more finely on a quality of recognition abilities, if they exist. Such an approach leads to more reliable results as shown by the present study.

These results also point to an important yet usually overlooked problem that pervades the brood-parasite literature in general and hampers our understanding of coevolutionary interactions: the need to divide continuous variables into discrete categories (Grim 2005). In theory, parasitic eggs are “mimetic” or “non-mimetic,” hosts are “acceptors” or “rejecters,” and adult parasites are “recognized” or “not recognized” by their hosts. In reality, there is a continuum of discrimination abilities along the continuum of resemblances. The present study documents how that phenomenon may confuse experimental results and their interpretations.

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