Natural born cheats:
Arms-races between cuckoos and their hosts

Tomáš Grim

Department of Zoology

Palacký University, Olomouc

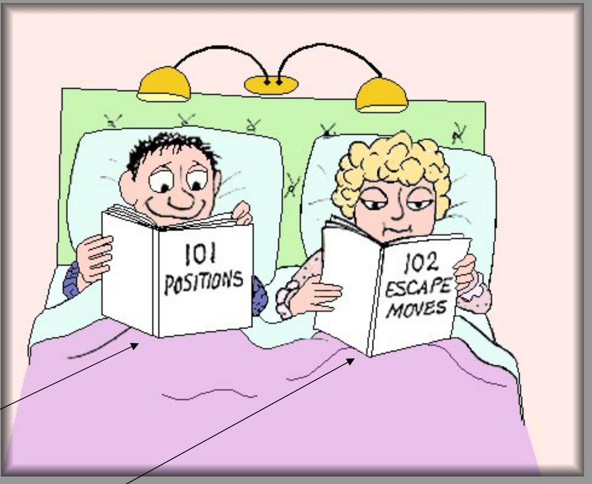
Human Frontier Science Program

General framework: Biological arms-race

	Host	**Parasite**
laying	aggression	cryptic & fast behaviour
incubation	egg rejection	egg mimicry
nestlings	chick rejection	chick mimicry

Dawkins & Krebs 1979: Proc. R. Soc.

General framework: Biological arms-race



adaptations & counter-adaptations

Dawkins & Krebs 1979: Proc. R. Soc.

Mimicry

Ecological races

Davies & Brooke 1989: J. Anim. Ecol.

What is the mechanism of mimicry?

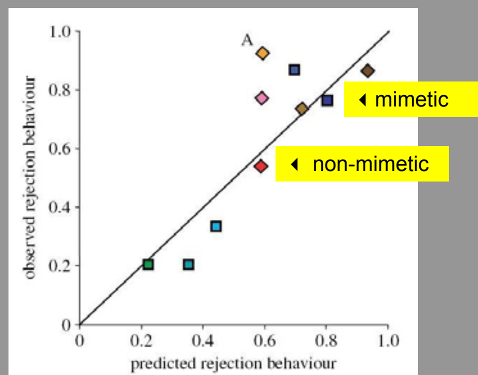
- ↘ chemical mimicry
- ↘ perceptual mimicry

- ↘ high performance liquid chromatography
- ↘ biliverdin, protoporphyrin
- ↘ conservative across species
- ↘ flexible within species

Igic et al. 2012: Proc. R. Soc.

Mimicry is only in the eye of the beholder

- ↘ visual modelling
- ↘ relevant observer - is never a human!



Cassey et al. 2008: Biol. Lett.

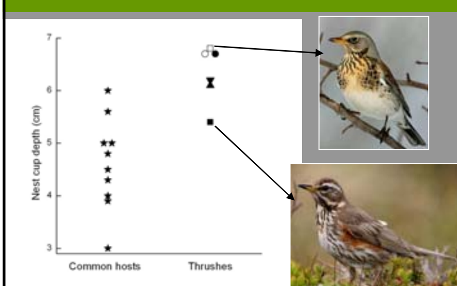
Integrative approach across all breeding stages: EU thrushes (*Turdus* spp.)

Absence/rarity of parasitism: alternative explanations

Host unsuitability	Cause	Coevolution
Primary	Life-history traits	No
Secondary	Anti-parasite defences	Yes

Soler et al. Oecologia 1999; Honza et al. J. Ethol. 2004

Life-history vs. co-evolutionary traits: common hosts *vs*. thrushes



Mann-Whitney P = 0.002

Welch t-test P = 0.0003

- ↘ mean masks species-specific differences
- ↘ **reification fallacy!**
- ↘ abstraction ≠ real thing
- ↘ exploratory comparison
- ↘ range vs. *particular* species

Grim et al. J. Anim. Ecol. 2011

Experiments: sympatry *vs*. allopatry

	Host	**Parasite**
laying	aggression	cryptic & fast behaviour
incubation	egg rejection	egg mimicry
nestlings	chick rejection	chick mimicry




Davies 2000: Cuckoos, cowbirds and other cheats. TA&D Poyser, London.

Material & data analyses
Meta-replication: space, time, phylogeny

- ↘ replicates
- ↘ spatial: 12 populations
- ↘ temporal: 1986-2009
- ↘ taxonomic: 4 *Turdus* spp.

- ↘ 1016 nests
- ↘ 1211 experiments

- ↘ generalized lin. mix. models

Bolker et al. Trends Ecol. Evol. 2009

1. line of defence: Are thrushes too aggressive?

- ⦣ low aggression and/or
- ⦣ cuckoo ≤ crow
- ⦣ sympatry ~ allopatry
- ⦣ thrushes < common hosts

Grim et al. J. Anim. Ecol. 2011

2. line of defence: Do thrushes reject alien eggs too often/fast?

- ⦣ rejection **frequency** ~50%
- ⦣ sympatry ~ allopatry
- ⦣ thrushes ≤ common hosts

- ⦣ rejection **latency** ~2-3 days
- ⦣ sympatry ~ allopatry
- ⦣ thrushes ≥ common hosts

Grim et al. J. Anim. Ecol. 2011

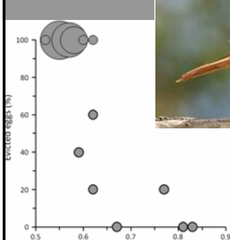
3. line of defence: Nestling stage

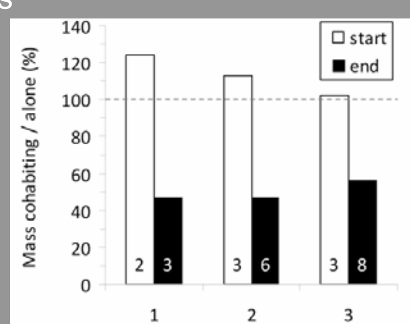
- unsuitable diet?
- defence ~ collateral damage

Grim Behav. Ecol. Sociobiol. 2006

Nest size, egg size and eviction success

- no effect of egg size per se
- strong effect of nest cup steepness (not nest size)
- nest architecture constraint
- forced competition with host chicks





Grim et al. Behav. Ecol. 2009; Grim et al. J. Anim. Ecol. 2011

Poor sample ≠ erroneous but unsure conclusions!

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*

Tomáš Grim[1] & Marcel Honza[2]

[1] *Laboratory of Ornithology, Faculty of Sciences, Palacký University, Tř*
mouc, Czech Republic; e-mail: grim@prfnw.upol.cz
[2] *Institute of Vertebrate Biology, AS CR, Květná 8, CZ-60365 Brn*
honza@brno.cas.cz

Grim, T. & Honza, M., Differences in behav
(*Turdus philomelos* and *T. merula*) towards
common cuckoo *Cuculus canorus*. Biologia, I
ISSN 0006-3088.

The common cuckoo *Cuculus canorus* parasit
common species sympatric with the brood pa
Potential host species may escape brood par
high rejection of cuckoo eggs or high aggre

	n	Effect size (%)
Blackbird	6	66.7
Song thrush	12	58.3

	n	Effect size (%)
Blackbird	208	65.7
Song thrush	84	54.2

Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011, **80**, 508–518 doi: 10.1111/j.1365-2656.2010.01798.x

Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts?

Tomáš Grim[1*], Peter Samaš[1], Csaba Moskát[2], Oddmund Kleven[3], Marcel Honza[4], Arne Moksnes[5,6], Eivin Røskaft[5,6] and Bård G. Stokke[5,6]

[1]*Department of Zoology and Laboratory of Ornithology, Palacký University, tř. Svobody 26, CZ–771 46 Olomouc, Czech Republic;* [2]*Animal Ecology Research Group of the Hungarian Academy of Sciences, c/o Hungarian Natural History Museum, H–1083 Budapest, Ludovika ter 2, Hungary;* [3]*National Centre for Biosystematics, Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway;* [4]*Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8, CZ–603 65 Brno, Czech Republic;* [5]*Department of Biology, Norwegian University of Science and Technology, NTNU, N–7491 Trondheim, Norway; and* [6]*Centre for Advanced Study, CAS, N–0271 Oslo, Norway*

Summary

1. Why are some common and apparently suitable resources avoided by potential users? This interesting ecological and evolutionary conundrum is vividly illustrated by obligate brood para-

Grim & Honza Biologia 2001 vs. Grim et al. J. Anim. Ecol. 2011

Sample size:
To maximize or to optimize?

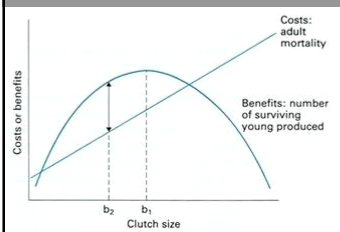
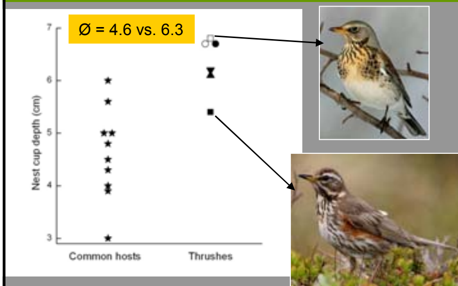


Fig. 1.6 The influence of adult mortality on the optimal clutch size. The number of young produced versus clutch size follows a curve, as in Fig. 1.5, with b_1 being the clutch size which maximizes the number of young produced per brood. Increased clutch size, however, has the cost of increased adult mortality, shown here for simplicity as a straight line. The clutch size which maximizes lifetime reproductive success is b_2, where the distance between the benefit and cost curves is a maximum. This is less than the clutch size b_1, which maximizes reproductive success per brood. From Charnov and Krebs (1974).

process, indicating scope for improvement. We should be aware of the fact that choosing sample size is an optimization process. 'The more samples, the better' is not a sensible strategy, because it may waste resources and undermine ethical concerns. The sample size used in a study can be too small, which would compromise statistical power and might render the research effort useless, and it can be too large: 'while wasting time and energy on badly designed experiments is foolish, causing more human or animal suffering or more disturbance to an ecosystem than is absolutely necessary is inexcusable' (Ruxton & Colegrave 2006, p. 4). There may be cases where very large sample sizes are required because the effect size aimed to be identified is obscure or intentionally small, the random variation in underlying data cannot be reduced by prudent experimentation, or because there are important ethical, economical or societal reasons to minimize the Type-II error (β). Such causes typically apply in medical research, where, for instance, the intended effects or side-effects of a new drug are to be scrutinized. In basic research on behaviour, however, these conditions might be rare, and the temptation to inflate sample size for unjustified reasons should be countered (Still 1982).

Taborsky Ethology 2010

Previous studies – traditional errors



- ↘ large body size
- ↘ large egg size
- ↘ large chick size
- ↘ diet composition
- ↘ ***general*** life-history traits
- ↘ a „thrush“ = logical error ...
- ↘ ... ***reification***
- ↘ species ***specific*** explanations

„thrushes“ are *primarily* unsuitable hosts

Moksnes et al. 1991; Kleven et al. 1999

Adaptive host selection

- ↘ categories – suitable/unsuitable
- ↘ *continuous* (un)suitability
- ↘ preference for *better* hosts

Kleven et al. Behav. Ecol. Sociobiol. 1999; De Mársico & Reboreda Proc. R. Soc. 2008

Traditional approach *vs.* the "thrush study"

- **single** model species
- **single** study population
- **single** ontog. parasite stage
- **single** hypothesis
- ignoring interactions
- comparisons **or** experiments
- **general** explanations

= typical characteristics of (behav.) ecol. studies!

- **taxonomical replicates**
- **spatial replicates**
- **all** ontog. parasite stages
- **multiple** hypotheses
- testing interactions
- comparisons **and** experiments
- species **specific** explanations

Grim et al. J. Anim. Ecol. 2011

Traditional approach *vs.* the "thrush study"

The Many Faces of Replication

Douglas H. Johnson*

ABSTRACT

Replication is one of the three cornerstones of inference from experimental studies, the other two being control and randomization. In fact, replication is essential for the benefits of randomization to apply. In addition to ordinary replication, the repetition of treatments within a study, two other levels of replication have been identified. Pseudoreplication, a termed coined by Stuart Hurlbert, generally involves making multiple measurements on experiment units (which is commendable) and treating them as if they reflected independent responses to treatment (which is erroneous). Metareplication is a higher level of replication in which entire studies are repeated. Scientists are too much concerned about analysis of data within studies and too little concerned about the repeatability of findings from studies conducted under a variety of conditions. Findings that are consistent among studies performed at different locations at different times with different investigators using different methods are likely to be robust and reliable.

Johnson 2006 USGS Paper 34

But why *un*suitable hosts *reject* parasitism?!

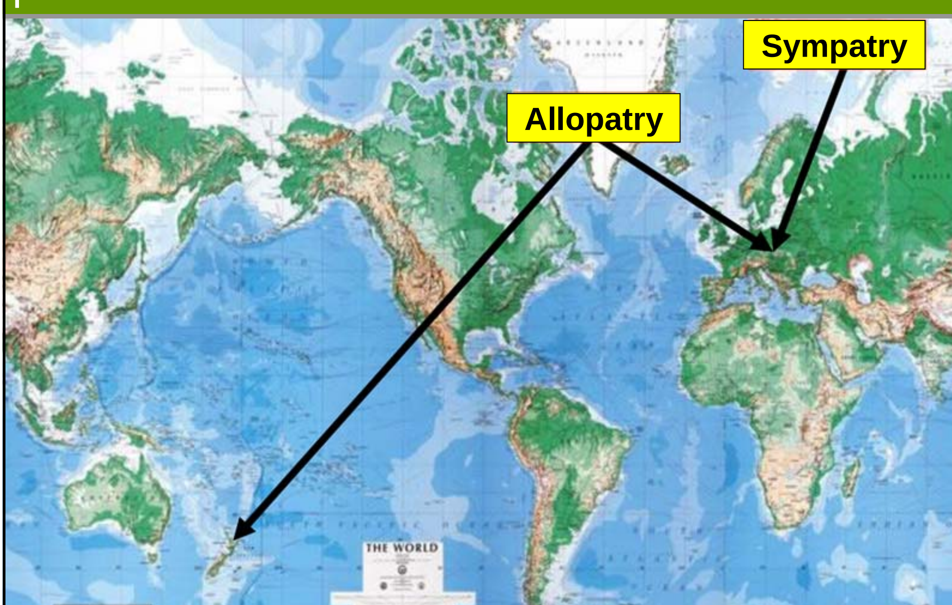
- ↘ interspecific parasitism (IP)
- ↘ conspecific parasitism (CP)
- ↘ IP + CP

- ↘ ghost of evolutionary past




Samaš et al. (MS)

Can we know the length of allopatry with parasites?

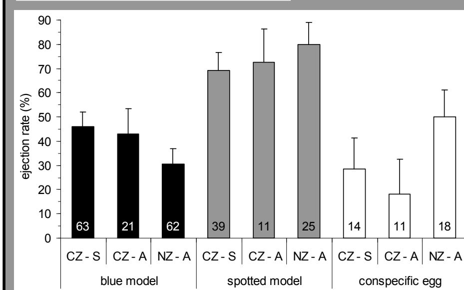


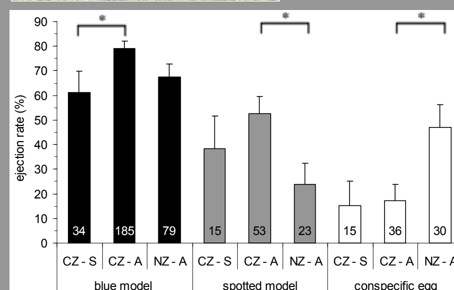
Predictions

	CP (thrushes)	IP (cuckoo)
Rejection of CP	+	–
Ejection costs/errors	+	–
Rejection frequency	S ≤ A	S > A
Latency to rejection	S ≥ A	S < A

Samaš et al. (MS)

Song thrushes and blackbirds reject up to 50% conspecific eggs!





Samaš et al. (MS)

Results

Nest desertion (~20%) is not a response to parasitism

	CP (thrushes)	IP (cuckoo)
Rejection of CP	+	
Ejection costs/errors	+	
Rejection frequency	S = A	
Latency to rejection	S = A	

Samaš et al. (MS)

Results

Nest desertion (~10%) is not a response to parasitism

	CP (thrushes)	IP (cuckoo)
Rejection of CP	+	
Ejection costs/errors	+	
Rejection frequency	S = A	
Latency to rejection	S = A	

Samaš et al. (MS)

Does it all make sense?

Host	Cuckoo	Energetic *cost* of rearing (unit: 1 consp. chick)
Reed warbler	Alone	6.45
Song thrush	Alone	2.11
	Cohabiting	0.15
Blackbird	Alone	0.06

In thrushes CP is *more* costly than IP!!!

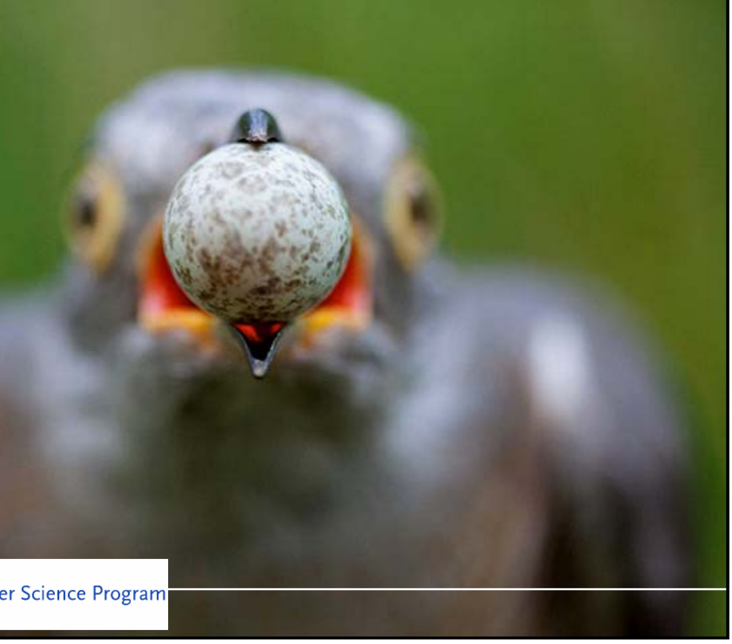
Grim (in prep.)

Lessons (we know them ... but forget too often:-)

- ↘ pseudoreplication
- ↘ metareplication ...
- ↘ ... space, time, phylogeny etc.
- ↘ sample size (benefits/costs)
- ↘ controls
- ↘ "multiple hypotheses"

... + Chamberlin Science 1890

Thanks



↘ fieldwork:
A. Dvorská
L. Polačiková
P. Procházka
P. Samaš
Z. Strachoňová

↘ Money:
HFSP Human Frontier Science Program