

Species Act, the Arctic Wildlife Refuge and federally owned lands in North America with widespread corruption but a range of success stories in the Old-World tropics (e.g. four new national parks have been gazetted in Tanzania alone within the past four years)?

Conclusion

Clearly, there is much to discuss. The re-wilding concept invites conservation practitioners to revisit the ecological and evolutionary targets that they want to shoot at; it calls paleontologists to work with conservationists in understanding stasis and change in Pleistocene ecosystems; it challenges captive-breeding institutions to rethink the conventional wisdom of keeping exotic species in the confinement of standard zoos, now under renewed scrutiny [13]; and it asks conservation biologists to reopen debate on the nature of the historical, geographical, genetic and ecological differences between past (re)introductions of California condors *Gymnogyps californianus* to Big Sur, wolves *Canis lupus* to Yellowstone, peregrine falcons *Falco peregrinus* from many continents to North America, south American cougars *Puma concolor* to the Everglades, wild turkeys *Meleagris gallopavo* to California; Arabian oryx *Oryx leucoryx* to Arizona; and African cheetahs to Texas.

On the other side of the coin, uncertainty about so many Pleistocene re-wilding issues; the understandable difficulties that its proponents have in facing these criticisms head-on using data; and conventional conservation dogma, backed up by pest biology, that novel introductions are hazardous for both ecological communities and agribusiness all argue against Pleistocene re-wilding. There is an air of desperation in the Pleistocene re-wilding idea to which we are all sympathetic. Conservation biology has developed into a science of documenting population

declines, species losses and habitat destruction in excruciating detail but sadly doing little about it. Pleistocene re-wilding is a proactive idea that could galvanize the conservation community out of its helplessness and, for that alone, deserves merit.

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A recognition-free mechanism for reliable rejection of brood parasites

Michael G. Anderson¹ and Mark E. Hauber²

¹ Ecology and Conservation Group, Institute of Natural Resources, Massey University, Albany Campus, Private Bag 102-904, North Shore Mail Centre, Auckland, New Zealand

² School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

Hosts often discard eggs of avian brood parasites, whereas parasitic chicks are typically accepted. This can be explained theoretically by fitness losses associated with adults learning to recognize parasitic young and mistakenly rejecting their own young. A new experimental study confirms that rejection of parasitic chicks, without relying on memory to discriminate between foreign and own young, is a feasible and potentially cost-free mechanism used by reed warblers to reject

common cuckoo chicks. By abandoning broods that are in the nest longer than is typical for their own young, parents can reliably reject parasite nestlings and reduce fitness losses owing to having to care for demanding parasitic young. Discrimination without recognition has important implications for the realized trajectories of host–parasite coevolutionary arms races.

Introduction

Social parasites exploit the foraging and breeding efforts of their hosts. Obligate brood parasitic birds, for instance, lay

Corresponding author: Anderson, M.G. (M.G.Anderson@massey.ac.nz).
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their eggs in the nests of other species and reduce the reproductive output of hosts that care for unrelated young. Despite fitness losses, hosts of some brood parasites, including *Molothrus* cowbirds, accept distinctive foreign eggs and chicks in their nest. By contrast, victims of *Clamator* and *Cuculus* cuckoos often reject parasitic eggs, despite the typically close visual match between foreign and host eggs [1]. The mimicry of host chick phenotypes is rare among the different avian brood parasite lineages [2], yet discrimination of parasite and host chicks by foster parents is even more infrequent [3,4]. How can foster parents in the few species where hosts do reject parasitic young, discriminate between their own and foreign chicks? In a recent experimental study, Grim [5] demonstrates that rejection of common cuckoo *Cuculus canorus* chicks by host reed warbler *Acrocephalus scirpaceus* parents is based on intrinsic differences in the duration of parental care required by broods of host versus parasite young.

Darwinian algorithms to reject parasites

The diversity of strategies by which avian brood parasites overcome host defences has offered one of the best opportunities for studying coevolution through observation and experimentation [1]. The cognitive processes used by hosts to defend against mimetic parasite eggs involve recognition through the assessment of the match between a learned template of own eggs and the phenotype of the potential parasite egg [6]. By contrast, theoretical models demonstrate that, even in the absence of costly neural structures associated with memory formation and storage, chick discrimination through learning might be maladaptive. This is because the cost of discrimination errors would be too high for both evicting and non-evicting cuckoo [7] and cowbird [8] chicks. Specifically, misimprinting on a parasitic young during the first nesting attempt by a host would lead to mistaken rejection of its own chicks in all subsequent broods.

In line with this theory, there are few reported examples of brood parasite discrimination at the nestling stage, although this might instead reflect less research effort in this area [9]. However, the experience of the hosts with raising young and, thus, learning about offspring, might not be required to identify parasites [4]. For example, just as memory might not be required to locate and benefit from caching seeds [10], the rejection of brood parasites might not require the recognition of foreign nestlings [3].

Nestling discrimination without recognition

Grim [5] illustrates how a custom-designed cross-fostering experiment can test between different proximate cues that are used by host parents. Initial observations revealed [3] that some common cuckoo chicks were abandoned during the advanced stages of the nestling period by reed warbler hosts. The recognition of nestlings based on phenotype alone (e.g. appearance or vocalizations) was unlikely as other experimental work already showed that reed warblers readily accept and feed heterospecific nestlings [11]. Three possible explanations for nestling rejection remained feasible: (i) the parental-fatigue hypothesis; (ii) the time-limit hypothesis; and (iii) the single-chick hypothesis (Box 1).

Box 1. Mechanisms of nestling rejection

For host parents to be able to reject brood parasite nestlings, some form of proximate cue is required to discriminate foreign chicks from their own nestlings. These can take the form of recognition-based (1) or recognition-free (2–4) mechanisms of discrimination.

1. Begging-call mimicry

Nestlings give begging calls when being fed by parents. These calls can vary between species and offer a cue that host parents can use to discriminate brood parasite nestlings. Brood parasites are able to counteradapt by mimicking the begging calls of their host [4]. Nestlings that do not show an acceptable level of vocal mimicry should be rejected near the age at which host chicks typically start to vocalize.

2. Parental-fatigue hypothesis

Parents might desert nestlings that require too much care to avoid excessive loss of future reproductive potential. This can occur if parasite nestlings require more food than does a brood of host nestlings. Parents might be physiologically unable to provide for the larger parasite nestling and so might either abandon when their exhaustion levels are too high or use the total amount of care required by young to discriminate between their own and foreign chicks. The desertion of parasite nestlings should occur once food provisioning levels are greater than the normal range observed for parents at unparasitized nest.

3. Time-limit hypothesis

Parasite nestlings fledge after a considerably longer period of time than do the offspring of their hosts, owing to the larger size of the parasites and the physiological constraints placed on their growth. Host parents can use this duration cue as a method to discriminate brood parasites from their own young [5]. Nestling rejection should therefore occur once the duration of parental care exceeds that required for host nestlings.

4. Single-chick hypothesis

Many brood parasite nestlings evict their nest mates, leaving a sole parasite chick for foster parents to feed. Brood loss could be used as a cue by parents to assess the risk for (partial) predation or to identify the nestling that they are feeding as a parasite. According to this scenario, broods with single nestlings should be disproportionately rejected. Nestling desertion should occur within the first few days of hatching, once a nestling is found to be alone in the nest after accounting for natural levels of hatching asynchrony.

Through a series of experiments, Grim and helpers created 'shortened' nests in which younger broods were swapped with older broods and 'prolonged' nests in which older broods were replaced with younger broods. Switching warbler chicks of different ages generated broods that received significantly extended or shortened parental care periods compared to what is typical for non-parasitized reed warbler broods (Figure 1). In addition, broods of four versus single warbler chicks were also generated, thereby creating variation in the overall amounts of care required for each brood within both shortened and prolonged treatments. Two types of nest served as controls: handling-only and cross-fostering of same age broods. The variations in the duration and the amount of parental care received then enabled the author to disentangle the three possible recognition-free mechanisms (Table 1).

The results on nest desertion rates were clear cut with regards to crucial predictions of the alternatives (Table 1). In support of the time-limit hypothesis, nest desertion only occurred in prolonged nests. A finding of similar rejection rates of single and four-chick broods was contrary to both



Figure 1. A typical brood of reed warbler chicks (depicted) demands much parental care. Broods of one or four reed warblers or a single common cuckoo chick that remain in the nest beyond the typical nestling period of the host, face abandonment by parents [3,5]. Reproduced with permission from T. Grim.

the parental fatigue hypothesis and the single-chick hypothesis. Furthermore, the single-chick hypothesis was also rejected because no desertions occurred in single-versus four-chick nests within either the shortened or the control treatments.

Desertions occurred in prolonged nests at a rate of 22% which closely reflected the observed desertion rate (15.8%) of nests naturally parasitized by cuckoos at the same study area [3]. This implies that similar proximate mechanisms for nest desertion might be utilized by natural and experimental foster parents. However, the average nestling age at which chicks died was lower for experimental broods with warbler chicks [5] than for sympatric, natural broods with cuckoo chicks [3].

Implications for host–parasite coevolutionary processes

Previous models of parasite rejection mechanisms led researchers to conclude that it would be maladaptive to learn to recognize nestlings for cuckoo hosts because of costly errors of accepting parasitic young and rejecting own young [7]. However, under this novel mechanism of discrimination without recognition, rejection errors are not made because nest abandonment occurs solely after the typical length of the host nestling period. In support of such a cost-free mechanism, Grim found no evidence at this research site for rejection errors where broods of reed warbler young were abandoned by parents [3,5]. Nonetheless, discrimination without recognition is not a strictly

cost-free rejection mechanism. This is because, in 78% of the cases, parents did fledge chicks from prolonged nests, thereby accepting the cost of longer parental care provided for experimentally ‘parasitized’ nests. Second, parents might not always reliably abandon parasitized broods in host species whose typical nestling period overlaps in duration with that of the nestling periods of the parasitic species [12].

Theoretical scenarios of coevolutionary arms races have also typically evoked escalating cycles between antiparasite defences by hosts and counteradaptations by parasites [1,4]. When foreign eggs are rejected because they look different, egg mimicry evolves [1]. In turn, when nestlings are rejected because their begging displays look or sound different, mimicry of begging behaviors evolve [4]. However, it appears that there is little defence against having a nestling period that is too long compared to that of the reed warbler, as common cuckoo chicks tend to have similar nestling periods regardless of host species size [13]. The absence of additional reduction in the duration of parasite nestling periods might represent the endpoint for any future coevolutionary process within this particular host–parasite system.

Alternatively, brood abandonment by reed warblers might represent a trait that evolved independently of cuckoo parasitism as a life-history tradeoff between current and future parental investment. If longer nestling periods are predictive of lower success of the current brood, owing to disease or weather-related slowing of growth, then parents might abandon current broods and attempt to breed later. Determining whether the abandonment by reed warblers of prolonged broods is a specific anti-parasite response will require conducting Grim’s experiments in genetically isolated populations of reed warblers that have never been exposed to brood parasitism, or in a series of a sister taxa of host and non-host species.

Recognition-free discrimination of brood parasites raises additional research questions and possibilities in coevolution and cognition. This mechanism not only shows that nestling discrimination is possible for evicting parasites raised alone, but also confirms that discrimination might not require prior learning or parental experience by hosts [4]. What then are the phenotypic and cognitive tricks used by single cuckoo chicks that cause naturally parasitized nests to be abandoned after a longer period of care than what is seen for experimentally prolonged broods of warbler chicks? And why did chicks in the shortened treatment consistently remain in the nest longer to receive more parental care than did control and prolonged host broods?

Table 1. Suggested mechanisms of brood abandonment in evicting brood parasites

Hypothesis	Age at abandonment ^a	Parasite mimicry expected	Reason for abandonment at given brood age
Recognition-based mechanism			
1. Begging call mimicry	4–5 days	Yes	Age when chicks begin to vocalize
Recognition-free mechanisms			
2. Parental fatigue	8 days	No	Age when the cumulative amount of provisioning by parent exceeds that required by brood of host
3. Time limit	12 days	No	Nestling period exceeds that of healthy host chicks
4. Single chick	1–3 days	No	Extent of maximum hatching asynchrony in host broods

^aA hypothetical host with a nestling period of 11 days.

Differences in the duration of parental care across treatments might be due to differences in the proximate, solicitation stimuli given by nestlings. The endogenous cues used by host parents to determine the appropriate duration of nestling care are also unknown. If the duration of parental care is under hormonal control [14] in reed warblers, it might be pertinent to test for hormonal titer differences between chick rejecters and acceptors. Most importantly, the causes of sensory and endocrine differences when responding to prolonged parental care would also need to be explored because, to date, we lack direct evidence about the genetic control of parasite-rejection mechanisms in any avian hosts [15], even though heritability and, thus, evolvability, of rejection decisions are pivotal assumptions of coevolutionary theory.

Conclusion

Our knowledge of the evolutionary diversity and frequency of nestling discrimination abilities by host parents has increased considerably over recent years. New findings add to this knowledge and offer several additional lines of research into the cognitive and physiological basis of recognition systems. They also suggest that the rules of nestling discrimination are varied and quite different from those of egg discrimination [7], inviting more research into the genetic, developmental, physiological and perceptual bases of host–parasite chick discrimination. These results will, in turn, be incorporated into evolutionary models of host–parasite systems and shape our understanding of the complexity of the arising coevolutionary processes.

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Letters

Maximizing the efficiency of conservation

Neal J. Hockley, Gareth Edwards-Jones and John R. Healey

School of the Environment and Natural Resources, University of Wales, Bangor, LL57 2UW, UK

We welcome Naidoo *et al.*'s recent review in TREE [1] highlighting the importance of measuring the costs of conservation directly, instead of relying on proxies, such as the area conserved. However, we are surprised that they advocate using biological proxies (e.g. the number of species conserved) to estimate the benefits of conservation, when calculating cost effectiveness. Similar to costs, the benefits of conservation, which include existence values, can be hard to measure, and we recognize that, by not directly considering benefits in the planning process, Naidoo *et al.* [1] reflect the prevailing tendency in conser-

vation [2]. Nevertheless, this approach concerns us for two reasons. First, we believe that measuring the benefits of conservation is no more difficult than collecting data on biological proxies, which could involve mapping the distributions of all species [3]. Second, irresolvable disagreement exists over the choice of which biological variables to maximize [3–5] and we are concerned that, in using these purely biological measures of conservation effectiveness, important value judgements are concealed.

Given that value is created by the interaction of humans with the environment, the benefits of conservation (similar to its costs) are anthropocentric. Although studies demonstrating the general importance of wild nature to humans abound [6], those examining the relationship between

Corresponding author: Hockley, N.J. (neal.hockley@univ.bangor.ac.uk).
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