Behav Ecol Sociobiol (2015) 69:1761–1767
DOI 10.1007/s00265-015-1988-8

ORIGINAL ARTICLE

Multiple mechanisms of egg recognition in a cuckoo host

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Received: 18 April 2015 / Revised: 25 July 2015 / Accepted: 3 August 2015 / Published online: 19 August 2015

Abstract The cognitive mechanisms behind egg rejection behavior have received increasing attention in recent years helping to understand the evolution of anti-parasite behavior by hosts. Here, we tested egg discrimination mechanisms of yellow-bellied prinia (*Prinia flaviventris*) in relation to different stages of egg laying (pre-egg laying, one host egg, and multi-host egg stages) and different extent of foreign egg mimicry (poor and high mimicry). We found that the prinia showed variation in egg rejection not only toward foreign eggs differing in mimicry but also among different stages of egg laying and within the same stage of laying. Prinias rejected 100 % of poorly mimetic foreign eggs in the pre-egg-laying stage, and 78.9 and 100 % in the one-host-egg and multi-host-egg stages, respectively. In contrast, they only rejected 38 % of highly mimetic eggs during the pre-egg-laying stage and accepted all at other stages. Multiple mechanisms, including a memory-based template through inheritance or learning, onset of laying, and direct comparison, may have evolved in the yellow-bellied prinia. The mechanisms depend on the mimicry of foreign eggs and the egg-laying stages tested. Innate or long-term memory template from previous breeding attempts may also be used in egg discrimination by hosts while observational learning or experience enhancement is involved in template formation, in which the first laying eggs may play a key role. However, discrimination during the pre-egg-laying stage may be a response toward foreign objects rather than parasitic eggs in this host species. These findings highlight the complexity of the multiple cognitive mechanisms involved in anti-parasite behavior.

Keywords Cognitive mechanism · Egg discrimination · Nest sanitation · *Prinia flaviventris* · Threshold of releasing behavior

Introduction

Egg rejection of alien eggs following recognition is one of the most important and general strategies that have evolved in avian hosts as a specific defense against brood parasitism that result in parasitism and often loss of reproductive success and the cost of parental care transferred to parasites (Davies 2011; Soler 2014). Egg rejection behavior is a specific anti-parasite adaptation that is a response to parasitism of hosts (Langmore et al. 2005). In other words, host species that historically have been in contact with brood parasites consistently possess the recognition capacity to perceive and distinguish alien eggs from their own eggs. However, the form and the extent of egg rejection behavior vary both among and within host species (Hauber and Sherman 2001; Moskát and Honza 2002; Yang et al. 2015). Furthermore, an individual host also presents variable reactions toward alien eggs with different mimicry under different conditions (Avilés et al. 2005; Holen and Johnstone 2006; Servedio and Hauber 2006). Therefore, consistency and flexibility coexist in the anti-parasite egg

Communicated by N. Clayton

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rejection behavior of hosts, which implies that both genetic and learning mechanisms may be involved (Lotem et al. 1995; Hauber and Sherman 2001; Martín-Gálvez et al. 2006; Moskát et al. 2010). So far, four kinds of mechanisms have been proposed to explain egg recognition behavior in hosts, including (1) direct comparison, (2) memory-based template, (3) onset of laying, and (4) phenotype distribution. Firstly, the direct comparison mechanism hypothesizes that hosts distinguish their own eggs from alien eggs by comparing these two types of eggs and reject the dissimilar outlier (Moksnes et al. 1991; Lotem et al. 1995; Marchetti 2000; Hauber and Sherman 2001; Bártol et al. 2002; Servedio and Lande 2003). The memory-based template mechanism assumes that hosts use a memory-based cognitive template of their own eggs to distinguish and reject alien eggs (Moksnes 1992; Hauber and Sherman 2001; Hauber et al. 2006; Yang et al. 2014a). Such a template may be formatted by observational learning (Lotem et al. 1995; Moskát et al. 2010) or inherited (Amundsen et al. 2002; Stokke et al. 2004). Alternatively, the onset of laying mechanism means that hosts use a rule of "any egg laid before me should not be mine" to reject the eggs laid prior to the onset of their own laying (Davies 2000). Finally, the phenotype distribution mechanism states that hosts use the appearance of the eggs laid by themselves to determine the trait distribution of their own eggs and to spot alien eggs whose phenotype falls outside this distribution (Servedio and Lande 2003).

Although egg recognition and rejection generally act as a consecutive process to discriminate alien eggs, they belong to perceptual and action components of egg discrimination, respectively (Moskát and Hauber 2007). However, the action component has received much more attention and empirical studies compared to that of the perceptual component (Liebert and Starks 2004; Mateo 2004). The perceptual process is critical for exploring the egg recognition mechanism and its evolution in brood parasitism-host systems (Rothstein and Robinson 1998; Lahti and Lahti 2002; Stokke et al. 2005; Hauber et al. 2006). Moskát and Hauber (2007) have performed a specific study to address this problem by comparing the rejection frequencies of alien eggs across consecutive egg-laying stages by great reed warbler (*Acrocephalus arundinaceus*), a major host of the common cuckoo (*Cuculus canorus*). Here, we conducted an empirical study with a similar procedure in another cuckoo-host system, in which the Oriental cuckoo (*Cuculus optatus*) lays highly mimetic brown eggs in the nests of yellow-bellied prinias (*Prinia flaviventris*) (Fig. 1). Compared to the study by Moskát and Hauber (2007) who only used mimetic alien eggs for experiments, here, we used both non-mimetic real eggs from a sympatric songbird, the common tailorbird (*Orthotomus sutorius*), and highly mimetic eggs (conspecific) to investigate the cognitive basis and its flexibility of egg rejection and the underlying mechanisms.

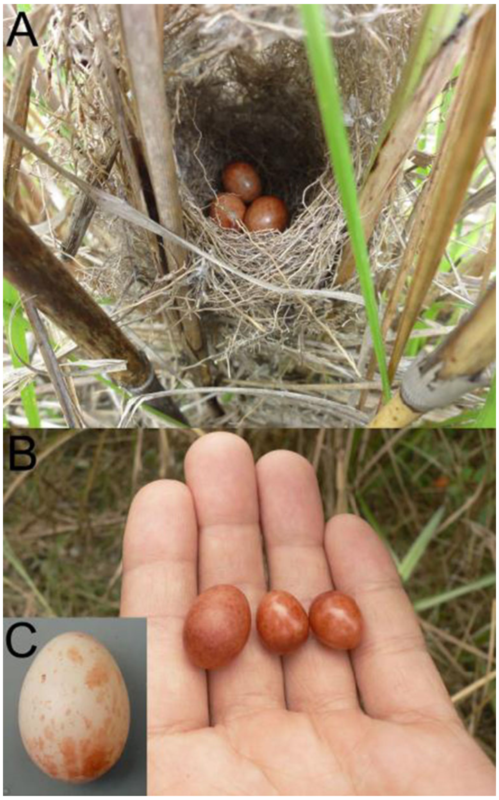

Fig. 1 Nest (**a**) and eggs (**b**) of the yellow-bellied prinia (the larger egg is the cuckoo egg), and poorly mimetic eggs from common tailorbird (**c**) used for parasitism experiment

Materials and methods

We performed this study in Nonggang National Nature Reserve (23° 39′ N, 107° 04′ E) at Guangxi, Southwest China, April–July 2012–2013. The yellow-bellied prinia is a common bird that lives and breeds in grasses and shrubs at a height of ca. 1 m. It lays eggs with highly dense brown markings that cover almost the entire eggs (Fig. 1), and it is parasitized by the Oriental cuckoo *C. optatus* with highly mimetic eggs (Yang et al. 2014b). In this study, we used eggs from the common tailorbird *O. sutorius* as poorly mimetic eggs for parasitism experiments (see in the next sections). The common tailorbird is a sympatric species in our study site, and it also lays eggs with brown markings, but the markings are much sparser than in eggs of the prinia (Fig. 1c). The tailorbird egg size was 1.03±0.07 cm^3 (n=20), which is not significantly different from that of prinia eggs (0.99±0.06 cm^3, n=20, t=1.89, df=37.3, P=0.067, Welch's t test). We searched for prinia nests across their typical nesting habitats and monitored their reproductive cycle. Observed nests were divided into two major groups of parasitism experiment: (1) poorly mimetic group (n=59 nests) and (2) highly mimetic group (n=47 nests). For the poorly mimetic group, poorly mimetic eggs from common tailorbirds were inserted into host nests and replaced one of the host eggs. For the highly mimetic group, conspecific eggs from other broods of prinia were introduced into host nests and replaced one of the host eggs. Both the poorly and the highly mimetic groups were sorted into three subgroups: (a) the pre-egg-laying group (n=21 nests for poorly mimetic nests and n=21 nests for highly mimetic nests), (b) the one-host-egg group (n=19 nests for poorly mimetic nests and n=13 nests for highly mimetic nests), and (c) the multi-host-egg group (n=19 nests for poorly mimetic nests and n=13 nests for highly mimetic nests). For the pre-egg-laying group, one foreign egg was inserted into each nest after nest building was completed but before egg laying. For the one-host-egg group, one foreign egg was introduced to replace the host egg on the day after the host laid its first egg. In this group, we tried our best to exchange the first host egg as soon as possible so the manipulation time was consistently at 7:00 a.m. just after the host laid its first egg. For the multi-host-egg group, one foreign egg was introduced to replace one of the host eggs after hosts laid two to five eggs (the maximum clutch size of the prinia is five eggs). Therefore, in this group, the experiment was conducted when two or more eggs were laid during the laying period or the clutch just completed, representing a situation that the hosts imprint on more eggs in their nests. Experimentally parasitized nests were monitored daily for 6 days to confirm the behavioral responses, which were classified as rejected if foreign eggs were ejected, buried or deserted, or accepted if foreign eggs were incubated (Moksnes et al. 1991; Moskát and Hauber 2007).

Linear mixed model was used for effect comparison (i.e., the effect of laying stages, rejection behavior, or egg mimicry on egg rejection) in this study while controlling for egg-laying date and clutch size. Statistical analysis was performed in IBM SPSS 20.0 for Windows (IBM Inc.).

Results

During two breeding seasons (from April to June) in 2012 and 2013, a total of 299 nests of the yellow-bellied prinia were found, but no nest was parasitized. The yellow-bellied prinia exhibited different rejection frequency toward poorly mimetic foreign eggs among different stages of laying ($F_{3,\ 43}$=285.87, P<0.001). It rejected 100 % (n=21), 78.9 % (n=19), and 100 % (n=19) of poorly mimetic foreign eggs during the pre-egg-laying, one-host-egg, and multi-host-egg groups, respectively (Fig. 2). A total of 50 % of rejection in the one-host-egg stage occurred after clutch completion. Furthermore, the rejection behavior also differed with 33 and 40 % of rejection events being desertion during the pre-egg-laying and one-host-egg groups, respectively, while all rejection events in the multi-host-egg group were by ejection ($F_{1,\ 41}$=238.62, P<0.001; Fig. 3). Additionally, for the pre-egg-laying and one-host-egg groups, the prinia rejected the poorly mimetic foreign eggs in various circumstances, including rejection without presence of own eggs, and rejection during laying own eggs or after clutch completion (Figs. 4 and 5). The prinia also expressed different rejection rates of highly mimetic foreign eggs among different stages of laying ($F_{3,\ 44}$=471.03, P<0.001). However, contrary to the poorly mimetic group, the prinia only rejected 38 % of highly mimetic foreign eggs in the pre-egg-laying group and accepted all highly mimetic foreign eggs in the one-host-egg and multi-host-egg groups (Fig. 2). Therefore, the yellow-bellied prinia responded differently to foreign egg with different extent of mimicry ($F_{1,\ 87}$=149.57, P<0.001) and during different stages of egg laying ($F_{2,\ 87}$=9.98, P<0.001).

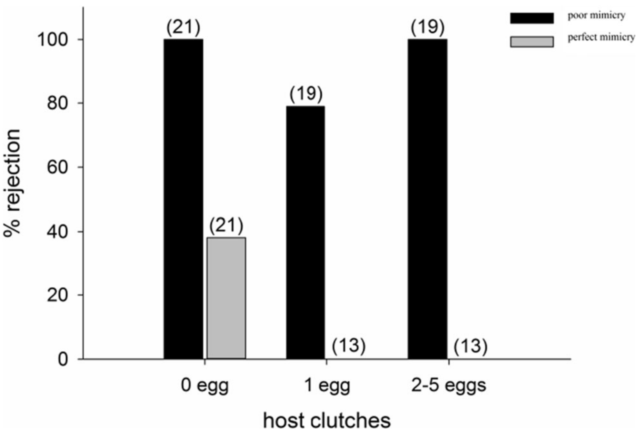

Fig. 2 Responses to poorly and highly mimetic foreign eggs in relation to number of host eggs when the parasitism experiment was performed. *Numbers in parentheses* on the bars refer to sample size

Discussion

According to our results, the yellow-bellied prinia showed variation of egg rejection not only toward foreign eggs

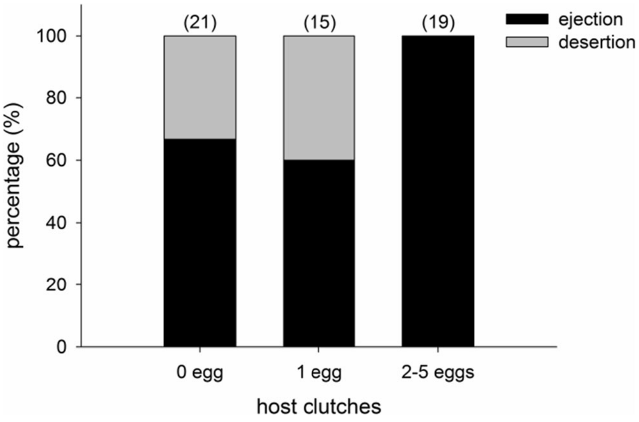

Fig. 3 Rejection types of poorly mimetic foreign eggs in relation to number of host eggs when the poorly mimetic parasitism experiment was performed. *Numbers in parentheses* on the bars refer to sample size

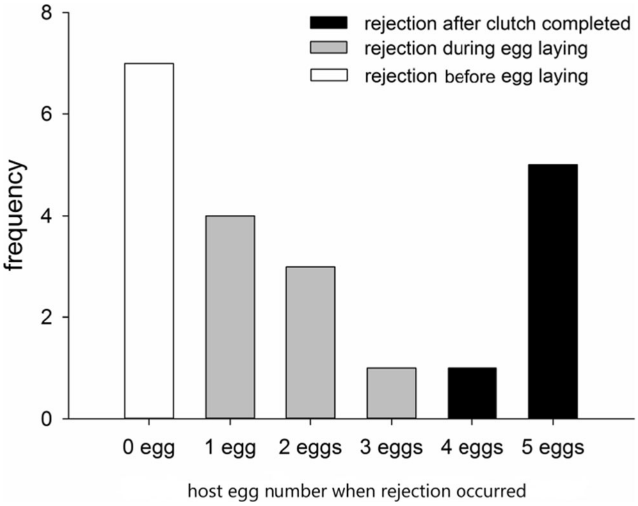

Fig. 4 Frequency distribution of rejection of poorly mimetic eggs in relation to host-egg number when rejection occurred during the pre-egg-laying stage

differing in mimicry but also among different stages and within the same stage of egg laying. The extent of foreign egg mimicry critically influenced whether and at which frequency foreign eggs were rejected from host nests. The host rejected all poorly mimetic foreign eggs during the pre-egg-laying and multi-host-egg stages and most poorly mimetic foreign eggs at the one-host-egg stage, but only rejected less than half of highly mimetic eggs during the pre-egg-laying stages and accepted all in the two other stages. The result for the poorly mimetic group indicated that hosts use the mechanism of memory-based template (Table 1) to recognize their own eggs and reject foreign eggs. Previous studies assumed that such a template might be inherited (Amundsen et al. 2002; Stokke et al. 2004), while observational learning may account for the formation of the recognition template in hosts (Lotem et al. 1995; Moskát et al. 2014a). Although rejecting all foreign eggs during the pre-egg-laying stage of the prinia illustrated that hosts use an innate or long-term memory-based template (learning from previous breeding attempts) for egg recognition (Moskát and Hauber 2007), our results supported that observational learning is involved in egg recognition during each breeding attempt because the prinia rejected fewer foreign eggs during the one-host-egg stage than at the other two stages, implying that the first own egg is critically important for the formation of a recognition template in hosts. In other words, although hosts possess a long-term memory-based template in their brain, they still need to enhance it in each ongoing breeding attempt to form an integrated template of its own egg phenotype to ensure accurate discrimination. Here, the first host eggs seem to play a key role in such observational learning of each breeding attempt. A previous study also supported this assumption because the yellow-bellied prinia lays eggs with a low intra-clutch variation as a defense against cuckoo parasitism (Yang et al. 2014b). Thus, the first egg is an important representation of the hosts' own egg phenotype. Therefore, parasitism at the one-host-egg stage forces some individuals to accept poorly mimetic foreign eggs because they may be confused or hesitating, as a result of tradeoff between the costs of breeding failure and mis-imprinting. Such individuals may belong to the young or inexperienced individuals in the population. Previous studies have found that the egg recognition capacity can increase with host age (Molina-Morales et al. 2014; Moskát et al. 2014a). Furthermore, in the rejection case during the one-host-egg stage, 80 % of rejection was conducted after hosts laid more eggs (from the second egg to the fifth egg) in their nests (Fig. 5), and 50 % of them occurred after clutch completion. These implied that prinia may need more time for egg comparison. For individuals that rejected foreign eggs before laying of the second eggs, 40 % were performed by desertion. This result supports our assumption above because most individuals need more of their own eggs as a comparison for rejection decision. Therefore, this result also partly supports the egg recognition mechanism of direct comparison (Table 1; Rothstein 1974; Feeney et al. 2014). An alternative explanation is that the increased checking of egg with time increases egg rejection when more host eggs have been laid.

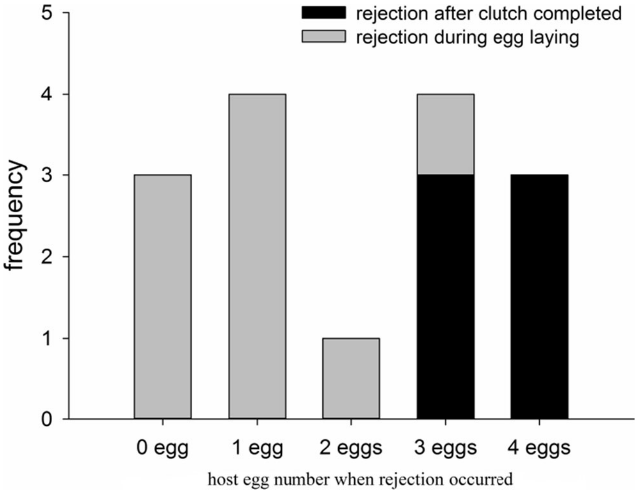

Fig. 5 Frequency distribution of rejection of poorly mimetic eggs in relation to host-egg number when rejection occurred during the one-host-egg stage

The response toward the highly mimetic foreign eggs in yellow-bellied prinias was different from that toward the poorly mimetic foreign eggs (Fig. 2). They only rejected a proportion of foreign eggs during the pre-egg-laying stage but accepted all foreign eggs at the other two stages. This result supports the egg rejection mechanism of the onset of laying (Davies 2000). Therefore, the prinia showed strong rejection toward both poorly mimetic (100 %) and highly mimetic (38 %) eggs during the pre-egg-laying stage compared to other stages, implying that the onset of laying mechanism is a significantly important strategy and more like an innate mechanism to counter parasitism. These results are contrary to a

Table 1 Variation in egg rejection rate during different laying stages as predicted by different cognitive mechanisms of egg discrimination (modified from Moskát and Hauber 2007), and the mechanisms supported by the results of this study

Stage of egg laying	Variation in rejection rate by different cognitive mechanisms			
	1. Direct comparison	2. Memory template	3. Onset of laying	4. Phenotype distribution
Pre-egg laying	Low	High	High	Low
One host egg	Low	High	Low	High
Multi-host egg	High	High	Low	Low
Responses of hosts (this study)				
1. To poorly mimetic eggs during three stages	–	Supported	–	–
2. To highly mimetic eggs during three stages	–	–	Supported	–
3. To poorly mimetic eggs during one-host-egg stage	Partly supported	–	–	–

previous study by Moskát and Hauber (2007), which found that the great reed warbler rejected significantly more parasite eggs during the one-host-egg stage, but had a considerably lower rejection frequency during the pre-egg-laying stage compared to the other stages of egg laying. They put forward a question why rejection frequency of hosts is not the highest against foreign eggs during the pre-egg-laying stage, which is free from ejection cost and error, and explained this phenomenon by the importance of observational learning and experience of hosts with their own eggs (Moskát and Hauber 2007). Here, we demonstrated that at least for the yellow-bellied prinia, the rejection of foreign eggs during the pre-egg-laying stage is the strongest compared to all other stages. Because learning and experience were also found to be involved in egg discrimination by the prinia, we suggested here that discrimination during the pre-egg-laying stage may be a response toward foreign objects rather than parasitic eggs. If hosts treat foreign eggs before egg laying as parasitic eggs, they need the memory template of their own eggs to spot parasitic eggs, but without their own eggs as comparison. However, if hosts handle the foreign eggs before egg laying as foreign objects, they can easily decide to reject them according to a much simpler rule that "anything that appears in my nest before me should be foreign objects." Therefore, in this host species, foreign eggs in nests during the pre-egg-laying stage trigger a behavioral action by nest sanitation, which may be an original behavior and pre-adaptation to egg discrimination (Rothstein 1975; Moskát et al. 2003; Yang et al. 2015).

The decision in egg discrimination may depend on the rank order of options for the hosts, which in turn rely on egg types (in this study mimicry), the number of eggs, or ratio of own eggs in host nests (Bateson and Healy 2005; Bán et al. 2013; Abernathy and Peer 2014a). Furthermore, egg discrimination can also be influenced by a variety of other effects including egg arrangement (Polaciková et al. 2013; Hanley et al. 2015), nesting stage (Moskát et al. 2014b), and the flushing of host parents (Hanley et al. 2015). Our study also has implications for understanding the difference in threshold of releasing behavior among different cognitive mechanisms, which has rarely been demonstrated before. According to our results, poorly mimetic foreign eggs more easily trigger egg rejection behavior than highly mimetic foreign eggs. However, egg rejection during the pre-egg-laying stage is strong toward both poorly and highly mimetic eggs compared to other stages of egg laying. Therefore, it is reasonable to infer that rejection during the pre-egg-laying stage is easier to trigger than at other stages of egg-laying. In other words, the threshold for releasing egg rejection behavior during the pre-egg-laying stage is lower than that during the other stages of egg laying. This is consistent with the former assumption that egg discrimination during the pre-egg-laying stage is triggered by nest sanitation behavior because an original behavior possesses a lower threshold for release within the same population or across different populations within the same species (Yang et al. 2015). Finally, it is worth to mention that perceptual modeling based on spectrophotometry, which can quantify egg mimicry based on avian vision, would provide a more reliable methodology for studying egg recognition mechanisms in hosts (Croston and Hauber 2014).

In summary, our study provides information for better understanding the cognitive mechanisms involved in egg rejection in brood parasite-host systems, suggesting that (1) multiple mechanisms may have evolved in hosts as a defense to counter brood parasitism, and the mechanisms involved depend on mimicry of foreign eggs used and the egg laying stages tested. (2) An innate or long-term memory template from previous breeding attempts is used in egg discrimination by hosts while observational learning or experience enhancement is involved in template formation, in which the first laid egg may play a key role. (3) Discrimination during the pre-egg-laying stage may be a response to foreign objects rather than parasitic eggs, and thus, it may be triggered by nest sanitation behavior. (4) Finally, the thresholds for releasing behavior differ among different stages of egg laying with the pre-egg-laying stage possessing a lower threshold compared to the other stages. We encourage further studies conducted to test these aspects.

Acknowledgments We would like to thank Ian Will, University of California, Berkeley, USA, Aiwu Jiang, Mingde Jiang, Qiuli Huang, and Yungao Hu for their assistance with the fieldwork. We thank Jianchou Nong and his family for help with the logistics. This work was supported by the National Natural Science Foundation of China (Nos. 31260514 to CY, 31272328 and 31472013 to WL) and Program for New Century Excellent Talents in University (NCET-13-0761) to CY.

Conflict of interest The authors declare that they have no competing interests.

Ethical standards The experiments comply with the current laws of China, where they were performed. Fieldwork was carried out under the permission of Nonggang National Nature Reserve, China. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University.

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