RESEARCH ARTICLE

Swiftlet Bacteriophages Concerning Diversity and Biological Features in South Kalimantan, Indonesia

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Abstract: We aimed to isolate and characterize bacteriophages infecting *Nitrobacter* spp. from swiftlet house environments and to evaluate their biological properties as potential biocontrol agents to mitigate nitrate accumulation in edible bird's nest (EBN) production. Environmental samples were collected from multiple swiftlet houses in South Kalimantan, Indonesia. Samples were enriched with *Nitrobacter* cultures, and bacteriophages were detected using spot assays followed by plaque purification. Plaque morphology was examined using digital microscopy. Host range specificity was assessed against a panel of nitrifying bacterial isolates obtained from different swiftlet houses. Phage replication dynamics, including rise period and burst size, were determined using one-step growth curve assays. Twelve distinct bacteriophages capable of infecting *Nitrobacter* were successfully isolated. Plaque morphologies varied from small, clear plaques to larger plaques with halos. Host range analysis demonstrated that all phages exhibited specificity toward *Nitrobacter* isolates. One-step growth curve analysis revealed rise periods ranging from 30 to 90 min and burst sizes spanning from 2.8 to 6429.9 plaque-forming units per infected cell, indicating substantial variability in replication efficiency among the phages. Bacteriophages isolated from swiftlet house environments displayed considerable morphological and biological diversity while maintaining a narrow host range for *Nitrobacter*. Phages exhibiting higher burst sizes represent promising candidates for targeted biocontrol strategies aimed at improving microbiological safety in EBN production. Further studies are required to evaluate phage stability, application feasibility, and integration into sustainable veterinary hygiene practices.

Keywords: Bacteriophage, Edible Bird's Nest, Swiftlet House, Veterinary Microbiology

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Introduction

Edible Bird's Nests (EBN), a food of animal origin produced by swiftlets (*Aerodramus fuciphagus*) from solidified salivary excretions, have been highly valued throughout Asia for their delicacy, nutritional benefits, and cultural importance [1]. Indonesia, the leading producer of EBN, is crucial in fulfilling worldwide demand [2]. In recent years, however, international trade of EBN has faced increasing regulatory and economic challenges due to concerns over excessive nitrate residues, which have resulted in stricter import requirements, shipment rejections, and financial losses for producers and exporters.

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The manufacturing process, from the swiftlet house to the consumer, has the potential for microbial risks that could threaten product quality and safety, affecting markets and business opportunities for producers [3].

Nitrifying bacteria, particularly *Nitrobacter*, represent a significant challenge in the EBN industry. These bacteria are commonly found in environments rich in nitrogenous waste and moisture, conditions that are characteristic of swiftlet houses due to the accumulation of droppings, residual feed, high humidity, and the presence of water sources. *Nitrobacter* spp. may colonize surfaces within swiftlet houses, including walls, nesting sites, and water reservoirs, and can be transferred to EBN during nest construction through direct contact with contaminated surfaces or aerosols. Once present, these bacteria catalyze the oxidation of nitrites to nitrates, leading to nitrate accumulation within EBN matrices [4]. Elevated nitrate levels degrade physical characteristics and raise food safety concerns, thereby preventing compliance with stringent export quality standards. Conventional microbial control measures in swiftlet houses are often impractical, disruptive to swiftlet behavior, or environmentally unfriendly, underscoring the need for alternative and sustainable interventions [5].

Bacteriophages are viruses that specifically target and destroy bacteria, offering a natural and effective approach to reestablish microbial balance while avoiding the use of chemical residues in the environment [6]. Its high specificity kills a specific bacterium, making it a great option for veterinary hygiene applications in food from animal-origin production systems. Although phage-based techniques have demonstrated efficacy in several agricultural [7, 8] and food safety applications [9], their investigation in EBN production has never been done.

Thus, we aimed to isolate, purify, and characterise bacteriophages that can infect *Nitrobacter* found in swiftlet house environments in South Kalimantan, Indonesia. We detected phages via spot assays and plaque purification, assessed morphological diversity using digital microscopy, evaluated host range specificity with various nitrifying bacterial isolates from distinct swiftlet houses, and analyzed the replication of phages using one-step growth curve evaluation. This study was designed to identify phage candidates with high specificity and beneficial biological characteristics for possible use as sustainable biocontrol agents in the future production systems of edible bird's nests.

Materials and Methods

Bacterial Isolates

Ten nitrifying bacteria isolates, including *Nitrobacter* sp. (n = 8) and *Acinetobacter bereziniae* (n = 2) (accession number: PX000574.1 and PX000546.1) were obtained from The Faculty of Veterinary Medicine, Universitas Wijaya Kusuma Surabaya. These isolates were used for the host range assay. All isolates were subcultured onto nutrient agar plates (Merck KGaA, Darmstadt, Germany) for 24 h at 28 °C.

Bacteriophage Isolation

Environmental samples, including pond water, sewage, and soil samples (n = 60), were collected from the swiftlet houses in South Kalimantan. Sampling followed standard environmental phage isolation procedures, in which 50 mL of water or 5 g of soil was aseptically collected into sterile containers [10]. Samples were transported on ice to the Laboratory of Veterinary Medicine, Universitas Wijaya Kusuma Surabaya, and processed within 24 h. Each sample was centrifuged at 10,000 × g for 10 min at 4 °C to remove debris, and the supernatant was filtered through a 0.22 µm Cellulose Acetate (CA) membrane filter (Millipore, USA). Ten milliliters of each filtrate were mixed with 10 mL of double-strength nutrient broth supplemented with 40 µL of 1 M $CaCl_2$ (Merck, Germany), 40 µL of 30 mM $(NH_4)_2SO_4$ (Merck, Germany), 40 µL of 6 mM Na_2CO_3 (Merck, Germany), and 100 µL of an overnight culture of *Nitrobacter* sp. strain AP6 (bacterial collection, Faculty of Veterinary Medicine, Universitas Wijaya Kusuma Surabaya). The enrichment cultures were incubated at 28 °C for 24 h. Following incubation, 5 mL of each culture was centrifuged at 15,000 × g for 10 min, and the supernatant was filtered through a 0.22 µm CA membrane filter. The resulting filtrates were used for phage detection using a spot test.

Spot Test

Phage activity was initially screened using the spot test method, following standard procedures for phage detection [11] The phage samples were serially diluted in Phosphate-Buffered Saline (PBS) (pH 6.7) up to 10^{-8} dilutions. An overnight culture of *Nitrobacter* sp. strain AP6 was prepared and mixed with 0.7% soft agar before being overlaid onto nutrient agar plates (double-layer agar method). The spot test was conducted by inoculating 10 µL of diluted phage sample onto a two-layer agar

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medium. Each plate underwent incubation for 24 hours at 28 °C. All samples with clear plaques were selected for further purification.

Purification and Phage Titer Determination

A plaque assay was used to purify phages and determine their titer as described in the recent bacteriophage protocol [12]. Six positive samples identified in the spot test were subjected to plaque purification. To ensure clonal purity, three consecutive rounds of plaque purification were conducted. In each round, a single well-isolated plaque was aseptically picked using a sterile pipette tip and resuspended in PBS (pH 6.7), followed by vortexing to elute phage particles. The suspension was serially diluted (10-fold up to 10^{-8}) and plated using the double-layer agar method by mixing diluted phage suspensions with 100 µL of an overnight *Nitrobacter* AP6 culture in 4 mL of 0.7% overlay agar maintained at 45 °C, which was then poured onto nutrient agar plates. Plates were incubated at 28 °C for 18–24 h. This process of single-plaque picking, resuspension, serial dilution, and re-plating was repeated for a total of three purification cycles. After the final purification round, a single plaque was amplified to obtain a high-titer phage lysate, which was used for subsequent analyses. The next day, each plate was visually examined for individual and distinct plaques, with 20-200 plaques/plate for morphology using a digital microscope, and calculating the plaque-forming units per milliliter (PFU/mL) using this formula:

$$\frac{Number\ of\ plaques\ counted\ (PFU)}{Volume\ plated\ (in\ mL)}\ x\ dilution\ factor = titer\ (PFU/mL)$$

Host Range

The host diversity of the isolated phages was evaluated using a panel of 10 nitrifying bacterial isolates, consisting of *Nitrobacter* sp. (n = 8) and *Acinetobacter bereziniae* (n = 2). Twelve distinct phages obtained from the purification step were tested. The assay was conducted utilizing the spot test method as previously outlined for evaluating phage host range [11]. All plates were incubated at 28 °C for 18–24 h. The presence of distinct plaques at the inoculation site was noted as a positive lytic reaction, whilst the lack of plaques was noted as negative. The host range profile of each phage was determined according to the quantity and classification of bacterial isolates lysed.

One-Step Growth Curve Assay

One-step growth curve assays were performed to ascertain the latent period and burst size of the selected phages, adhering to conventional techniques with minor modifications [13]. In summary, 3 mL of an overnight bacterial culture was added to 27 mL of nutrient broth (Merck KGaA, Darmstadt, Germany) and incubated at 28 °C for 18 h. Ten milliliters of the culture were distributed into 15 sterile tubes (triplicate). Each tube was infected with 100 µL of phage suspension at a minimum titer of 1×10^9 PFU/mL and incubated on ice for 10 min. Following centrifugation (15,000 × g, 5 min), the supernatants were subjected to filtration using 0.22 µm pore-size CA membrane filters, and the pellets were resuspended in 10 mL of new nutrient broth.

At predetermined time points (0 s, 30 s, 1, 5, 10, 15, 30, 60, 90, and 120 min), 1 mL aliquots were collected from the infected cultures in triplicate and immediately placed on ice to halt further phage development. Once all the time points were completed, the tubes were centrifuged at 21,000 x g for 5 min. The supernatant was filtered using a 0.22 µm pore size CA membrane filter and stored at 4 °C. The filtrates were serially diluted (10-fold, up to 10^{-10}). Phage titers were determined by the double-layer plaque assay. The period of latent activity is defined as the duration between adsorption and the onset of the increase in phage titer. The burst size was calculated as the ratio of the total phage titer to the initial phage count, expressed as a percentage.

Results

Bacteriophage Isolation and Plaque Morphology

We successfully isolated 12 distinct phages from pond water, sewage, and soil samples (n = 60) from the swiftlet houses in South Kalimantan. Based on the spot test, six samples contained phage against *Nitrobacter* sp. Figure 1 presents six samples of the positive result for the spot test in this study. All positive samples were selected for the purification step using a plaque assay. Based on the plaque assay, 12 distinct phages have been purified and show high titer (Table 1) against *Nitrobacter* sp.

These phages had a range of morphologies, including clear plaques and clear plaques with halos (Figures 2 and 4). Halo zones were seen in 58.3% of isolates, and plaque sizes varied from 1.37 to 11.40 mm (Table 1, Figures 3-4). Distinct plaque development on the host bacterial lawn indicated that all of the separated phages exhibited lytic activity against the *Nitrobacter* strain. These results demonstrate the variety of plaque morphologies and provide confidence in the phages' possible use as efficient biocontrol agents.

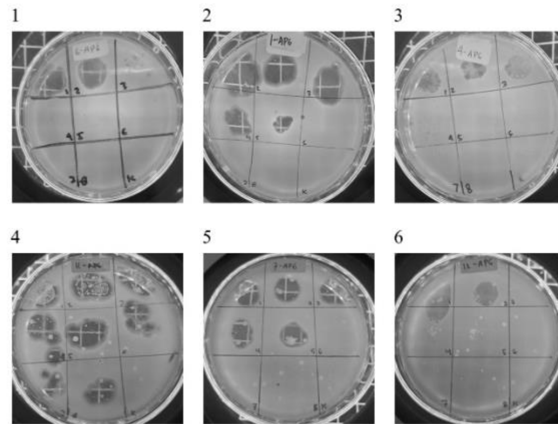

Fig. 1: The six positive results from environmental samples using the spot test

Table 1: The bacteriophage isolation from sewage, soil, and pond water of swiftlet houses in South Kalimantan.

Isolate code	Origin	Titre (PFU/mL)	Plaque morphology	Plaque size average (mm)
1-AP6	Sewage	2.6×10^7	Clear halo	8.93
2-AP6	Soil	2.4×10^8	Clear halo	10.40
3-AP6	Pond water	2.0×10^9	Clear halo	7.69
4-AP6	Pond water	2.6×10^6	Clear	1.37
5-AP6	Sewage	2.8×10^6	Clear	1.84
6-AP6	Sewage	1.5×10^7	Clear	1.40
7-AP6	Sewage	1.3×10^7	Clear halo	7.70
8-AP6	Sewage	2.0×10^8	Clear halo	8.87
9-AP6	Sewage	1.0×10^8	Clear	4.20
10-AP6	Sewage	3.7×10^6	Clear halo	8.90
11-AP6	Soil	2.0×10^9	Clear halo	11.40
12-AP6	Sewage	1.8×10^6	Clear	2.00

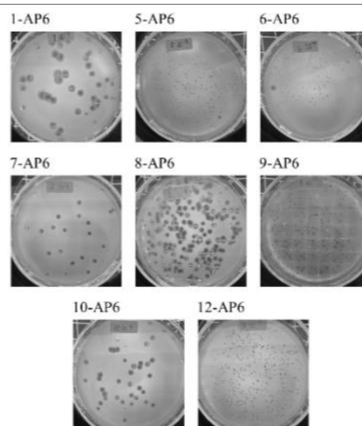

Fig. 2: The plaque assay results from sewage samples

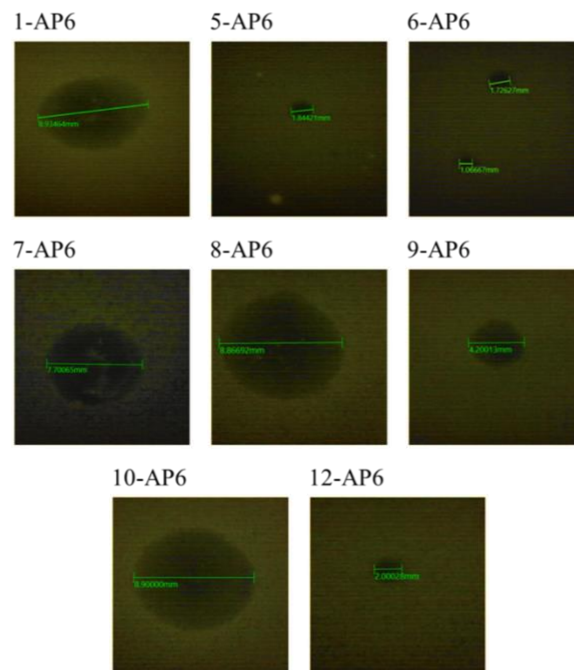

Fig. 3: The various plaque sizes from sewage samples

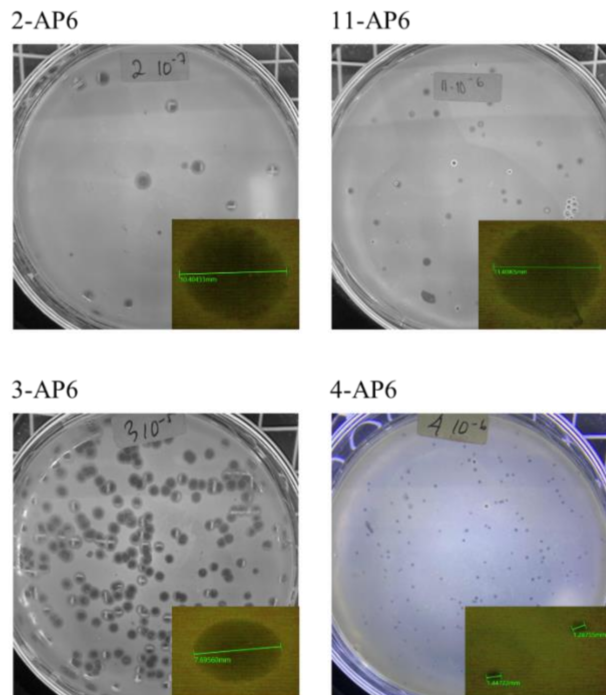

Fig. 4: The plaque assay results from soil (2-AP6 and 11-AP6) and pond water (3-AP6 and 4-AP6)

Phage Host Range Determination

The host diversity of the isolated phages was assessed using a panel of 10 nitrifying bacterial isolates, involving 8 *Nitrobacter* sp. and 2 *A. bereziniae*. All phages showed lytic activity against the *Nitrobacter* isolates (100%); however, no lysis was observed against *A. bereziniae* (Table 2). The findings demonstrate that the isolated phages exhibit high specificity for *Nitrobacter*, indicating their potential use as targeted biocontrol agents in swiftlet house environments.

Table 2: The phage host range results

Phages ID	*Nitrobacter* sp. (n = 8)	*Acinetobacter bereziniae* (n = 2)	Host range summary
1-AP6	+	–	Specific to *Nitrobacter*
2-AP6	+	–	Specific to *Nitrobacter*
3-AP6	+	–	Specific to *Nitrobacter*
4-AP6	+	–	Specific to *Nitrobacter*
5-AP6	+	–	Specific to *Nitrobacter*
6-AP6	+	–	Specific to *Nitrobacter*
7-AP6	+	–	Specific to *Nitrobacter*
8-AP6	+	–	Specific to *Nitrobacter*
9-AP6	+	–	Specific to *Nitrobacter*
10-AP6	+	–	Specific to *Nitrobacter*
11-AP6	+	–	Specific to *Nitrobacter*
12-AP6	+	–	Specific to *Nitrobacter*

Note: (+) lysis observed; (–) no lysis observed. All phages infected *Nitrobacter* isolates (100%), while no activity was detected against *A. bereziniae*

One-Step Growth Curve Analysis

A one-step growth curve analysis was performed to evaluate the replication dynamics of the isolated phages (Figure 5). The latent time varied from 0 to 30 minutes, succeeded by a rise phase of between 30 and 90 minutes. The mean burst size exhibited significant variability among isolates. The data reveal significant variability in the replication capacity of the phages, with certain phages demonstrating high productivity, indicating their potential as effective candidates for *Nitrobacter* biocontrol in swiftlet house settings.

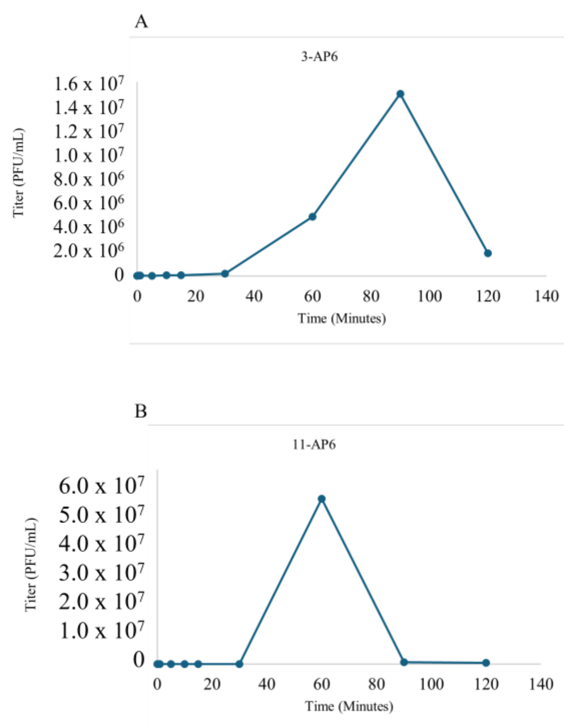

Fig. 5: One-step growth curves of bacteriophages isolated from pond water (A) and soil (B). Phage replication dynamics were determined by monitoring the number of plaque-forming units (PFU) per milliliter over time. The latent period ranged from 0 to 30 minutes, followed by a rise period of 30–90 minutes. Burst sizes varied among isolates, ranging from 2.8 to 6429.9 PFU per infected cell

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Discussion

This work presents the original, carried-out investigation into bacteriophages present in swiftlet house habitats in South Kalimantan, emphasizing their morphology, host range, and replication dynamics. Twelve unique phages were successfully isolated from environmental materials, each exhibiting lytic activity against *Nitrobacter* sp. The results highlight the biological diversity of phages in these environments and indicate their potential applications as biocontrol agents to reduce nitrifying bacterial contamination in Edible Bird's Nest (EBN) production.

Plaque morphology serves as a significant phenotypic indicator of phage diversity and activity [14]. The observed variance, from clear to halo plaques (Figures 2-4), indicates changes in lytic capacities and potentially the synthesis of depolymerase enzymes, which destroy extracellular polymers and contribute to host cell infection [15]. The occurrence of halos in 58.3% of isolates indicates the probability of enzymatic activity, aligning with results from prior phage investigations focused on bacterial pathogens in agricultural production [16].

The determination of host range (Table 2) indicated the high specificity of all identified phages for *Nitrobacter* sp., exhibiting no lytic activity against *A. bereziniae*. Narrow host ranges may restrict the wider use of phages; yet, they offer benefits for targeted biocontrol, reducing off-target impacts on non-pathogenic or beneficial bacteria like *A. bereziniae*. This host specificity corresponds with prior research indicating that the majority of phages can infect only a restricted range of strains within a bacterial species. [17]. From a practical standpoint, the strict lytic activity against *Nitrobacter* is advantageous, as nitrate accumulation in swiftlet habitats has been linked to diminished EBN quality and market viability.

The one-step growth curve analysis (Figure 5) revealed substantial heterogeneity in phage replication dynamics, with latent periods ranging from 0 to 30 min and burst sizes spanning from 2.8 to 6429.9 PFU per infected cell. While this broad range highlights functional diversity among *Nitrobacter*-infecting phages, the extremely low burst size observed for one phage (2.8 PFU/cell) warrants specific consideration. Such a low burst size is atypical for strictly lytic phages and may reflect an inefficient or incomplete lytic cycle, potentially arising from suboptimal adsorption efficiency, delayed or partial genome replication, premature host lysis, or host physiological constraints under the experimental conditions. Although plaque morphology analysis revealed halo formation in several phages, this feature was observed in both low- and high-burst-size phages, indicating that halo formation alone does not directly correlate with replication efficiency in this study. The presence of halos may therefore reflect localized diffusion dynamics or extracellular enzymatic activity that is independent of intracellular phage production. Consequently, while plaque morphology provides useful phenotypic information, it should not be interpreted as a proxy for burst size or lytic productivity without additional supporting data. Future studies integrating quantitative correlation analyses, adsorption kinetics, and genomic characterization of genes associated with lysis and extracellular matrix degradation are needed to elucidate the mechanistic relationship between plaque morphology and phage replication dynamics.

Although no evidence of lysogeny was detected, this result suggests that phage–host compatibility and infection efficiency may vary considerably even within a narrow host range. In contrast, the very high burst sizes observed for other phages indicate highly productive infections and support their suitability for rapid biocontrol applications. These findings underscore that phages infecting the same bacterial genus can exhibit markedly different life-history strategies, as also reported in phage therapy studies [18], and highlight the importance of evaluating individual phage performance rather than grouping replication parameters into a single generalized profile.

This work highlights the ecological and functional adaptability of bacteriophages in swiftlet house habitats, shown by the diversity of plaque morphologies, limited host range, and varying replication dynamics. From a practical perspective, our findings establish a basis for the creation of phage-based biocontrol techniques intended to enhance the microbiological quality of EBN. Future research should concentrate on the genetic characterisation of these phages, assessment of their stability in swiftlet houses, and evaluation of their effectiveness in mitigating nitrate accumulation in the environment.

Conclusion

The identification of halo-forming plaques in over fifty percent of the isolates indicates potential depolymerase activity, which could be significant in eliminating *Nitrobacter*. The one-step growth curve demonstrated significant heterogeneity in replication techniques, with latent durations ranging from 0 to 30 minutes and burst sizes varying from 2.8 to 6429.9 PFU per infected cell. This variation indicates functional specialization, wherein high-burst-size phages may act as effective agents for

the fast reduction of *Nitrobacter*. Concurrently, phages with reduced burst sizes may contribute to the preservation of long-term ecological stability. This study offers comprehensive insights into the biological characteristics within the distinctive ecological niche of swiftlet houses. In addition to enhancing scientific knowledge, our findings possess practical importance because phage-based therapies could reduce nitrate accumulation attributed to *Nitrobacter*, hence enhancing the quality and market value of edible bird's nest (EBN). These measures provide an effective and economically applicable strategy for strengthening Indonesia's EBN industry in the global market.

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Author's Contributions

Siti Gusti Ningrum: Idea Generation, Procedure, Control, Data Collection, Formal Investigation, Original Draft Writing, Review and Editing of Manuscript.

Hana Cipka Pramuda Wardhani: Investigation, Methodology, Data Collection, Validation.

Intan Permatasari Hermawan: Research, Data Management, Formal Assessment, Drafting – Analysis and Revision.

Ethics

This study did not include human or animal subjects and, hence, did not necessitate ethical approval. The authors declare that the data presented is original.

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