國立臺灣大學國際學院生物多樣性國際碩士學位學程

碩士論文

Master's Program of Biodiversity
International College
National Taiwan University

Master Thesis

金門栗喉蜂虎身體素質與寄生蟲感染評估

Body Condition and Parasite Prevalence Assessment of Blue-tailed Bee-eaters (*Merops philippinus*) in Kinmen

Rajatanan Prapatsorn

指導教授：袁孝維 博士

Advisor: Hsiao-Wei Yuan, PhD

中華民國 112 年 7 月

July, 2023

doi:10.6342/NTU202302673

國立臺灣大學碩士學位論文
口試委員會審定書
MASTER'S THESIS ACCEPTANCE CERTIFICATE
NATIONAL TAIWAN UNIVERSITY

金門栗喉蜂虎身體素質與寄生蟲感染評估
Body Condition and Parasite Prevalence Assessment of Blue-tailed Bee-eaters (*Merops philippinus*) in Kinmen

本論文係 Rajatanan Prapatsorn (R10H44004) 在國立臺灣大學生物多樣性國際碩士學位學程完成之碩士學位論文，於民國112年7月17日承下列考試委員審查 通過及口試及格，特此證明。

The undersign, appointed by the Department / Institute of Master's program in Biodiversity on 17 July 2023 have examined a Master's thesis entitled above presented by Rajatanan Prapatsorn (R10H44004) candidate and hereby certify that it is worthy of acceptance.

口試委員 Oral examination committee:

指導教授/Advisor

系主任、所長 / Director :

Acknowledgments

Starting over to pursue a different career path when you're in your mid-thirties (with a considerably stable job) is challenging. It takes away your confidence of being just *good enough* by the fact that your younger peers are more capable of doing things and how smart they are. However, I am here, as a master's student at one of the world's best universities where I can confidently say I am proud to be. Firstly, I would like to express my sincere gratitude to National Taiwan University and the Biodiversity Program who gave me the great opportunity to be able to learn, share, and enjoy the campus life again.

I am deeply grateful to my advisor, Professor Hsiao-Wei Yuan, for her guidance, insight, and her generous support. Without her reassuring encouragement and mentorship, I couldn't have shaped my master's thesis and would have been lost in the sea of anxiety and confusion. I extend my appreciation to Professor Yuan's lab members for giving me a warm friendship and a brilliant working environment. I am greatly appreciate Han-Bo Chang and Yun-Xuan Lin for their knowledge, expertise, and their constructive feedback on Kinmen's summer fairies, the blue-tailed bee-eater. The extra time they spent discussing with me has significantly contributed to my understanding of the subject matter and has shaped the direction of my research. I had a lot of precious memories shared with them and will never forget their supports.

I would like to express my gratitude to all my MPB classmates for sticking together through high and low tides as I believe everyone will overcome the obstacles before us and of course, I wish all of us will be successful in the path we choose. I give my special thanks to Carina Terry and Ashanti McKoy, the most wonderful women who provide me unlimited morale and a safe space where we can act silly together. Thank you the otter boy, Chung-Hao Ruan, for his generosity and recognition of who I truly am without judgment. The handyman, Wei-Che Tsai, who can be almost anything including a bird guide, a personal driver, and a little brother who I enjoy bickering with. Thank you Mary Noer and Bill Terry for their hospitality and unconditional love every time I was in Taichung. I will continue this spirit of kindness by paying it forward.

I am profoundly grateful to my mother, the only one in our family who always supports my decision regardless of what other people say. I am indebted to her dedication to push me further towards what achievement I have in mind.

And lastly, I want to express my heartfelt gratitude to my dearest friend who I could not imagine what kind of person I would become without her mental support, Biyoke Madavisid. Thank you for your compassion, understanding, and unwavering belief that I am *good enough*.

doi:10.6342/NTU202302673

Abstract

Several studies have proved that birds residing in higher density colonies had more chance of infectious disease exposure. Not only parasite infection deteriorate host physical condition, it also indirectly affects the reproductive performance which can affect the population stability. Kinmen island, known to be the only breeding ground of blue-tailed bee-eater (*Merops philippinus*) within Taiwanese territory, has been removing vegetation periodically to attract more birds to breed in the destined areas. As a result, those areas showed to host higher bird density than the untreated colonies nonetheless its population health has yet been investigated. This study aimed to compare parasite prevalence, body condition, and reproductive performance between birds breeding in natural and treated colonies to determine whether human intervention in effort of conservation has any impact on bee-eater health. The study found that despite birds residing in natural colonies expressed better body condition and brood size, there was no significant difference in parasite prevalence between the colony types. Moreover, none of pathogen infection had significant influence over the body condition nor reproductive performance. This study findings which was in opposition to the initial expectation might be elicited by low disease prevalence, migration strategy, and natural selection. Without any serious health concern, the blue-tailed bee-eaters population in Kinmen island was in acceptable condition thus far. Human intervention by breeding grounds alteration did not have critical impact on its population health and reproductive performance.

Keywords: blue-tailed bee-eater, prevalence, parasite, body condition, brood size, breeding colonies

doi:10.6342/NTU202302673

Table of Contents

doi:10.6342/NTU202302673

Lists of Figures

doi:10.6342/NTU202302673

Lists of Tables

doi:10.6342/NTU202302673

Introduction and literature review

Many bird species form nesting colonies to benefit from breeding synchronization reducing the chance of being attacked by their predators as well as forming the community aiding in better foraging (Picman et al., 2002; Ward & Zahavi, 1973). However, living in a colony also brings challenges to the animal including competition for resources and territory and a higher risk of infection. These costs can consequently affect the overall well-being of both parents and their chicks where birds living in larger colony size may find it harder to find food and suffer more disease exposure. Some studies suggested colonial breeding might put the species into more vulnerable situations than the benefit they get.

Effect of colony density on infection risk and immune response

Although increasing nest density may promote the population of summer breeders, colony density can cause negative effects on the birds expressing high sociality as well. The risk of infection in congregated bird colonies was proved to be higher than in the lower-density colonies due to the higher rate of horizontal transmission of various parasites. This circumstance can be explained by the frequent individual contact among the hosts (Møller et al., 2001). Previous literature meta-analysis indicated a positive correlation between host group size and prevalence, as well as intensity. Another similar study, by comparing multiple published studies of sister species that had overlapping distribution, habitats, and migratory patterns, found that the prevalence of blood parasites was higher in colonial species than their solitary breeding sister species (Côté & Poulinb, 1995; Tella, 2002). The study of insect parasite transmission in 2004 indicated that there was a greater likelihood of external parasite and virus transmission where the colony size

doi:10.6342/NTU202302673

increased in cliff swallows as a consequence of transient birds introduced into the colony (Brown & Brown, 2004; O'Brien & Brown, 2011).

Some studies also investigated mixed-species breeding colonies where the prevalence might be influenced by the occurrence of multiple species. A study conducted in Castro Verde Special Protection Area, Portugal found that the abundance of the most common parasite, *Carnus hemapterus*, was influenced by single host species nest number rather than the overall nest density of mixed species (Gameiro et al., 2021). A stratified multi-level analysis in different study units from an individual level to a community level in forest passerines found a strong positive correlation between mean *Philornis* larval abundance and the density of suitable hosts where an increase in host density caused increasing parasite abundance in the community level (Manzoli et al., 2013).

Not only a direct impact on avian health, but population density can also cause immunity alteration. Parasite collection from 13 species of swallows and martins showed the heavy investment in nestling immune function in colonial species which relatively prolong their development, therefore the extension of parasite exposure (Møller et al., 2001). Other studies supported the immunity investment were conducted by cross-fostering young chicks in different colony sizes in waterbird species, the offsprings raised by larger colony showed the chicks had higher heterophils/lymphocytes ratio and lower phytohaemagglutinin (PHA) response, indicating higher parasite loads and lower immunocompetence respectively due to elevated social stress level. Chicks from larger colonies were in poorer condition and slower growth rate (Kaminski et al., 2021; Minias et al., 2019; Minias et al., 2015).

doi:10.6342/NTU202302673

Effect of infectious disease on body condition and survival rate

Infectious disease in birds cannot be overlooked since it can bring devastating effects to wildlife population monitoring and conservation. Many infections deteriorate the host's physical condition and alter the immune response. These are important features necessary for migratory birds which demand high fitness during migration. High severity of some infections may also cause death, especially in nestlings, leading to lower survival rates and fledging success in chicks.

External parasite, blood-sucking parasites in particular, is one of the most common and most harmful pathogens in wild birds. Some of the most common blood-sucking external parasites are northern mites (*Ornithonyssus sylviarum*) and red mites (*Dermanyssus gallinae*) which they distribute worldwide and all avian species are susceptible. Birds affected with mites often show anemia and poor body condition. Bloodsucking mites also transmit several infectious diseases including viral and bacterial infections which cause death (Schuster & Krone, 2016). A study found that European bee-eater chicks with blood-sucking flies (*Carnus hemapterus*) infestation had slower growth rates than uninfected chicks (Hoi et al., 2010). The same author also investigated in later years that there was a negative effect of flies on nestlings' body condition and immune response where they were improved significantly if the parasites were removed (Hoi et al., 2017). A study of the native nest flies (*Philornis* spp.) myiasis impact on Ridgway's hawks breeding success indicated that the hawk nestlings affected by parasitism had lower survival rates than the chicks treated by topical insecticidal. Moreover, infested nestlings are prone to have less fledging success as well (Hayes et al., 2018).

doi:10.6342/NTU202302673

Intestinal parasites are considered to be common pathogens detected and affect a wide range of wild species. Birds infected by intestinal protozoa and worms show some concerning symptoms including loss of appetite, therefore loss of weight. These signs often present with severe diarrhea which could lead to death (Schuster & Krone, 2016).

Another important parasite that has been widely studied and globally spread in bird populations is Haemosporidian parasite, or the so-called "Avian Malaria". Three important genera which are known to cause disease in birds include *Haemoproteus*, *Leukozytozoon,* and *Plasmodium*. Although most infected birds show asymptomatic signs, a heavy pathogenic infection can cause severe disease, as well as death, can possibly occur. In general, birds infected with avian malaria show common signs of fever, anorexia, weight loss, and anemia to the severity of its diffusion to all organs causing failure and death (Ilgūnas et al., 2016; Williams, 2005). A comparative study between urban and rural bird residents showed one remarkable observation that there was a negative correlation between body condition and *Haemoproteus* infection density in Canyon Towhee (Bobby Fokidis et al., 2008). Although there was no incident of human infection by any avian malaria parasites, there is still an obscurity of the possibility of cross-infection from birds to humans. With the flexibility to switch between hosts, an ability to switch reproductive strategies, and several reports of malaria species infecting human close relatives, avian malaria cannot be excluded as a zoonotic threat (Clark & Taylor-Robinson, 2021).

An ex-situ inverse investigation by using a medication experiment in a high *Haemoproteus* prevalence population of Blue tits (*Parus caeruleus*) found that the proportion of nestling mortality in the unmedicated control group was lower than in the medicated group. At the end of the experiment, the infection intensity as well as the

doi:10.6342/NTU202302673

female body mass in the control group was significantly lower (Merino et al., 2000). An alternative approach to investigate Haemosporidian prevalence and vector abundance influence on Pied Flycatchers (*Ficedula hypoleuca*) health, with regard to the proximity of water bodies, found that their body condition was lower in the vicinity of water sources. In addition, the adult's body mass was significantly become lower closer to the water bodies at the end of the breeding season. This can also be implied that Haemosporidian infection can cause health deterioration over time exposure (Krams et al., 2022).

Co-infection of two or more avian malaria shows to have a greater impact on bird survival than a single infection. An infection survey in house martins (*Delichon urbicum*) showed the infection had a significant influence on survival rate where the individuals double-infected by chewing lice had the lowest chance to survive. Double infection also burdened the birds to have the lowest body mass compared to single infection and uninfected individuals (Marzal et al., 2008). The survey was in congruence with the survey that co-infection with Haemosporidian decreased the survival possibility of Great tits (*Parus major*) in Switzerland (Pigeault et al., 2018). Haemosporidian infection in young birds usually results in a poorer survival rate compared to adults, which leads to lower fledging success in several bird species (Merino et al., 2000; Sol et al., 2003; Townsend et al., 2018).

Effect of infection and physical fitness on reproductive performance

In general, parasitism in animals reduces the host's fitness while the parasite survives by exploiting the host's resources. This pathological pathway where the parasite impairs or alters the host's ability to function and utilize their resources gain efficiently, leads to the host's deteriorating overall health in consequence. Not only does parasitism directly cause physical strains in birds, but subsequent physiological stress from infection

doi:10.6342/NTU202302673

also induces more chances of susceptible infection and alters the reproductive performance to compensate for the negative energy balance (Blas, 2015; da Silva Rodrigues et al., 2021). One example was a significant correlation of natural gastrointestinal nematode load on the reproductive success of female wild European shags (*Gulosus aristotelis*) by a 30% decrease in fledging success (Hicks et al., 2019). However, the relation between either infection status or body condition and reproductive success, whether it is direct causation or not, is still ambiguous.

Annual average breeding success was significantly correlated with the condition of male Blue petrel (*Halobaena caerulea*). Together with both sexes conditions and males experience, which had significant influence on the decision to breed, in response to their reproductive strategy (Chastel et al., 1995). Furthermore, better parental body condition indices reflecting on energy reserves show a higher probability of more chick survival rate and fledging success. Relatively heavier parents also produced about three times more independent chicks as well as their body condition (Milenkaya et al., 2015; Pigeault et al., 2019).

Importance of population health and reproductive success in conservation

Research on breeding birds forms the highest share of reports. It reflects population dynamics and persistence in which breeding success provides valuable information for interpretation. Many studies also showed that reproductive success and adult survival contribute most to population dynamics (Cuthbert et al., 2014; Nuijten et al., 2020; Rönkä et al., 2011). As mobile links are crucial for maintaining ecosystem

doi:10.6342/NTU202302673

function, monitoring the abundance and distribution of bird populations as well as reproductive performance is essential for long-term conservation plans.

The relationship between animal health, reproduction rate, and population maintenance is inseparable. Health and reproductive success are important factors for the survival of wildlife populations. During the breeding seasons, there is a remarkable trade-off between parental health and investment in raising their offspring. Particularly in migratory birds, individual fitness plays an important role in breeding decisions where they have to manage their energy allocation wisely. Imbalance energy spending on either of those can cause changes in immune response where an increase in infection risk occur (Reséndiz-Infante & Gauthier, 2020; Stope, 2023). Infection has contributed to species decline as well as limited its ability to remain sustainable populations. Increasing disease prevalence and severity in wildlife populations leads to a higher chance of extinction. (Russell et al., 2020).

Burrowing bird species such as bee-eaters play an important role of strengthen biodiversity by providing nesting and habitats as well as resources to other secondary cavity nesters and other living organisms. As a result, various species using bee-eater nests increase interspecific interaction and augment the more complex ecosystem. Mining activity of bee-eaters also enhances an ideal setting for abiotic processes and makes the soil more sensitive to climate factors, particularly in arid areas (Casas-Crivillé & Valera, 2005). Therefore, besides the economic benefits as a tourist attraction, sustaining the blue-tailed bee-eater population on Kinmen island is also a valuable asset for the island ecosystem.

doi:10.6342/NTU202302673

Area introduction

Kinmen island is one of the important migratory birds stopping points situated within the Republic of China (Taiwan) territory. The island is also known as the only place where Blue-tailed bee-eaters (*Merops philippinus*) spend their summer breeding and raising their chicks. Named after their bright and colorful feathers, these renowned summer fairies promote the island to become a popular destination for bird enthusiasts in recent years. With being one of the important military posts in Taiwan, Kinmen alone welcomed around 2.5 million tourists in 2019 (Wong, 2021).

The blue-tailed bee-eater

Blue-tailed bee-eater (*Merops philippinus*) is a non-passerine bird belongs to the family Meropidae, containing three genera and thirty species. The bee-eaters distribute widely in Africa and Asia, with some species in southern Europe, Australia, and New Guinea. Its current population trend was stable and is listed as Least Concern (LC) by IUCN Red List (IUCN, 2016).

The bird has a distinctive green plumage with blue tail, thin black mask, and a rufous throat while the juvenile has similar characteristics but paler, with a tannish throat and shorter tail; lacking the adult's elongated central tail feathers. Male and female plumages are usually similar. The birds have long and curved downward bills which allow them to catch flying insects.

Blue-tailed bee-eaters often prefer the beach or sand dunes to dig their nest burrows with less vegetation preferred (Yuan et al., 2006). Burrows seen on sand piles of construction sites and farm ponds were reported as well. The nesting burrows are 1-2 m deep with 6-8 cm in diameter of the tunnel. The oval-shaped nesting chamber lies at the

doi:10.6342/NTU202302673

end of the tunnel where 2-7 eggs will be laid (Yuan et al., 2006). Eggs are laid at least a week after completion of the nest tunnel within the nesting period, from hatching to fledging, which ranges from 24 to 36 days, and often fledge synchronously according to the breeding biology of related species (Boland, 2004). From previous on-site observation, blue-tailed bee-eaters residing on Kinmen island normally fledge around the end of July to early August.

Maintaining the bird population in Kinmen island had been regulated for years by the National Park office by altering the sand loams according to previous studies of bee-eater nest fidelity and preferences. The treated breeding colonies where vegetation and soil surface are removed had 3.1 times higher active nests than the unaltered colonies and also showed greater density (Wang et al., 2009). Therefore, many bird-watching sites are altered at least once a year during late spring to early summer to attract the migratory blue-tailed bee-eaters by park management. According to the past survey from the year 2015 to 2021, birds residing in treated colonies usually had 3-4 times more active nests than the natural colonies with higher nest density per colony.

Past observation, questions, and hypotheses

Active nest counts of blue-tailed bee-eater nests in Kinmen island indicated that there was a population fluctuation in the past decade when it reached the peak number in 2019 with 1,867 total nest counts. Nonetheless, the total nest number deliberately declined and reached the lowest number of 1,352 nests in 2021. Yet the blue-tailed bee-eater population health status on Kinmen island has never been investigated. To understand the mechanism behind the blue-tailed bee-eater declining population trend, as well as to

doi:10.6342/NTU202302673

maintain the sustainable population size on this island, an underlying infection that may affect overall health and reproductive success should not be overlooked.

This study will concentrate on the comparison between natural colonies and treated colonies, where the sand slopes are regularly altered by the national park, and whether there are differences in body condition and reproductive performance of the two populations. Studies indicated that the more dense colony is, the risk of infection would likely to be higher. Therefore I formulated three hypotheses as follows:

1) According to the aforementioned studies, a higher parasite infection rate in treated colonies is expected.

2) As a consequence of parasitism on avian health and reproduction, the infected birds should show poorer body condition and lower reproductive performance as well as the more severe impact of co-infection of two or more parasites can aggravate the health outcome.

3) In corresponding with the first and second hypotheses, birds residing in treated colonies are likely to have poorer body condition and reproductive performance.

4) Regardless of infection status in the overall bird population, the birds that show poorer body condition should have lower reproductive performance.

doi:10.6342/NTU202302673

Methodology

Sites and study species

All data was collected from Kinmen island, the only place within the Republic of China (Taiwan) territory where it hosts blue-tailed bee-eaters to breed during summer. Most bee-eaters are gregarious and social. The clan-type community forms cooperative breeding behavior which involves assistance from non-breeding adults or sub-adults. The most important function of helpers is to bring food to the nestlings, sometimes helping the parents dig the nests. Bee-eaters come to Kinmen Island around early summer (April - May) and usually choose the breeding location where they have reproductive success from the prior year, as known as site fidelity (蔡佩妤, 2007).

Breeding colonies were classified into two categories which are 1) natural colonies where there was no landscape adjustment prior to the bird's arrival and 2) treated colonies where the sand loams were altered by the Kinmen National Park. Treated colonies were remolded by shaving the surface of the slope to clean out the vegetation, then compacting the slope with backfill earth. All slopes are altered with an excavator at least twice a year, usually in December and February, before the birds arrive. The purpose of this protocol is to make sure that the breeding slopes are vegetation cleared. Furthermore, after getting soaked by rainfall and drying out, the sand loams will be more condensed preventing them to be collapsed during the breeding season. Using the previous data of the nest survey in 2021, the landscape and nests number of each acknowledged colony were re-assessed starting from mid-June to mid-July 2022.

Seven most populated colonies were chosen. All colonies were situated near the shore except for two treated colonies. The samples were collected from four natural and three treated colonies between June to July 2022. All 137 samples were collected from

doi:10.6342/NTU202302673

adult blue-tailed bee-eater birds residing in each sand loam with consideration of the possibility to catch without disturbing the nestlings. The lists of all colonies, the nest number, and the nest density of each are shown in Table 1 (page 71). Although the southern side of Oucuo beach was another natural colony where a high number of active nests were observed, this site was not included in the collection due to time constraints. Moreover, this particular area was preferred to be in undisturbed condition. The treated colony called Triangle Castle (TC) was composed of five small to medium size colonies (ranging from 7-89 nests). All colonies were adjoined into one colony since each colony was within walking distance and the birds were believed to share the same foraging area.

Active nests reassessment was conducted by using micro-lens attached with LED white light and 2 meters wooden pole. The camera was connected to the LCD monitor to evaluate the nest status in the bee-eater's burrows. Nest status was classified into four stages including egg, hatchling, sheath, and nestling according to the stage of growth of the chicks.

All stages in one nest were counted and recorded in total number as “brood size”. The definition of nestling stages is as follows:

Stage	Definition
Egg	Shell is still intact. No or small sight of crack observed.
Hatchling	Early stage of nestling early emerging from its egg. Undeveloped or barely seen newly developed pin feather. Usually seen with closed eyes and limited movement.
Sheath	More pin feather developed. Some are fully developed. Eyes fully opened and more vigorous movement, but still cannot fly.
Fledgling	Fully developed brownish to green feather without the elongated central tail feathers. Some can make a short flight.

doi:10.6342/NTU202302673

Since the nest count and nest status of all destined locations could not complete within one day, the date of observation was also included in the record for further analysis.

Samples collecting criteria and measurement

Catching criteria were determined to ensure a higher possibility to capture the adults on the next day. At least one parent was presenting or the majority of the nest was composed of eggs and/or hatchlings are the main criteria. These criteria implied a higher chance of the parents staying in the burrow the next morning (capture day). Marker flags were put in front of the appointed nests.

All Blue-tailed bee-eaters were captured during the early morning between 5 AM - 9 AM. The burrows with the marker flags were re-examined again by using micro -lens with wooden pole. If at least one parent is presenting, a hoop net (approximately 30 cm. in diameter) secured with metal hooks will be placed at the nest entrance. The bird was detangled immediately after the capture was spotted, put an animal in a fabric string bag separately then kept them in the cool shade.

For the breeding colony where the hoop net could not be placed due to the exceeding of humans reaching heights or its environment was considered to be fragile such as in YFL and TC, mist nets will be applied as an alternative. Birds were removed and kept in the holding bag immediately after being caught on the net. Tricolor code was painted on each bird's tail using the harm-free color markers and identified its nest later on the same day. The nest location was confirmed by taking a photograph of the bird while entering the burrow and matching the location with the printed nest map. The nest was observed once again by micro-lens to confirm the chick stage.

doi:10.6342/NTU202302673

Each captured adult was banded by a metal ring with engraved individual code and color code to keep track of its annual population and migration. The length of the head, bill, tarsus, wing chord, tail, and streamer was measured using a vernier caliper and wing ruler. Bird weight was measured using a small digital scale. General physical examination including external parasite detection and body condition score assessment were performed by a certified veterinary practitioner.

Scale mass index (SMI) and body condition score (BCS) were used as data indicating the body condition or physical fitness in this study. Though the body mass alone was validated as an acceptable indicator for bird body condition (Labocha & Hayes, 2011; Nip et al., 2019) however, the SMI was recommended as a more precise indicator in terms of energy reserves relative to size (Peig & Green, 2009). The SMI of each bird was computed and employed in statistical analysis later. Each individual was recorded with its brood size as the main reproductive performance indices. Recaptured birds' BCS and weight were also recorded without the predisposed information of the previous capture.

Sample collection methods

Fecal samples were collected by two methods. If the feces was seen around the capture area, on the animal itself, or in the string bag, a direct fecal swab was performed accordingly. Cloacal swabs were applied only in the case in which the bird did not defecate spontaneously by using a small q-tip and saline irrigation. All fecal samples were stored in microcentrifuge tubes at 4 degree Celsius.

Blood samples were obtained by venipuncture on the brachial vein using a 27-1/2 gauge needle attached to a 1 ml tuberculin syringe, then stored in heparinized tubes at 4

doi:10.6342/NTU202302673

ºC. The total amount of collectible blood was 0.3 ml maximum or no more than 1% of body mass (Jimenez-Penuela et al., 2019).

Two kilograms of sand from the 3 old burrow nests from the north side of Oucuo beach (OCN) were collected to investigate the breeding site environment. The samples were spread in a thin layer (1 cm) to the plastic sheet by midday. The insects moved to the surface were collected with hand forceps and kept in ethanol filled container for later microscopic examination (Hoi et al., 2010).

Samples examination

Fecal samples were examined within the same day of the collection to prevent bacterial overgrowth which can alter the number of parasites therefore infection severity evaluation. All fecal parasites were detected by the fresh smear method despite the recommendation of using the fecal flotation method to identify the parasite eggs (Lagrue & Presswell, 2016) since fecal samples collected from bee-eaters were less than the amount required for this detection technique. Two small amounts of bird dropping were placed on the same microscopic slide (duplicate examination). One or two drops of saline were added in case the sample was still solid, then covered the samples by coverslips. Each slide was examined and evaluated for pathogen severity under the light microscope at 40X - 400X magnification. The concerned pathogens included fecal helminth, protozoa, and opportunistic spirochete infection.

Duplicated blood smears of each individual were fixed in methanol and stained using commercial Romanowsky stain (Diff-Quik) on the same day of blood collection. All samples were let dry before storing in a slide box and examined for avian blood

doi:10.6342/NTU202302673

parasites not limited to Haemosporidian (Avian malaria) under a light microscope at 1000X magnification.

All parasite species identification was omitted since the microscopic method appears to have low sensitivity. For example, Plasmodium gametocytes are usually mistaken for the large gametocytes of *Haemoproteus sp*. Therefore, these two Haemosporidians could not be distinguished solely from light microscopes (Clark et al., 2009).

Parasite prevalence, body condition, and infection severity validation

Each parasite detected from individual samples was calculated to estimate the prevalence by percentage. Parasite prevalence in this study was defined by the proportion of a population infected by parasites in a given time period. The prevalence was calculated as follows:

Prevalence = number of samples infected / total number of samples in a population

Following the guideline by Peig & Green (2009), the scale mass index (SMI) was computed after knowing each individual's body mass as follows:

$$\text{scaled mass index: } \hat{M}_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

where M_i is body mass in grams and L_i is the linear body measurement of the individual (i). In this study, tarsus length was used to represent the linear body measurement since it was the most corresponding index to body weight. The b_{SMA} is the scaling exponent estimated by the SMA regression of M on L where L_0 is the average tarsus length of the population. $\hat{M}_i$ is the predicted body mass for each bird individual.

doi:10.6342/NTU202302673

Body condition score (BCS) is a way to assess physical condition. In general, it is one of the mandatory protocols to evaluate general fitness in medical practice worldwide. There are several scoring systems widely used in aves, however, only pectoral muscle scoring was applied in this study. Pectoral muscle can be observed from the top view to estimate the sharpness of the keel ridge (breast bone), the shape and size of breast muscle relative to the keel, and fat coverage over the sternum. Then allocate all criteria into a numeric score (Doneley, 2016).

In this survey, five scores system was adapted from the simpler three scales of the Great tit (Gosler, 1991) and a more modernized seven scales of budgerigars (Burton et al., 2014). The scores range from 1 to 5 where the minimum represents emaciated (score 1) and the maximum represents obese (score 5). Interpolated intermediate values (±0.5) were also used in this survey. Details on the score criteria are shown in Table 2 (page 72). Scoring was estimated by one observer to prevent discrepancies from multiple evaluators.

External parasite was graded using an absent and present score. Any detection of external parasites on a bird's feathers and skin was considered as present. All external parasites were identified and recorded.

Intestinal worms (helminth) score was assigned. According to the detection method used in this study, a fecal fresh smear was relatively insensitive which implied that false negative results may occur. The total float method was suggested to be the gold standard of helminth egg detection in animals according to the previous study (Lagrue & Presswell, 2016). However, this method required at least 3 grams of bird dropping. It is impossible to obtain this amount of sample from bee-eaters. Therefore, helminth was graded using absent and present scores. Any detection of eggs or larvae either within duplicated slides will be considered as present.

doi:10.6342/NTU202302673

Fecal protozoa trophozoites, cysts, or oocysts and spirochete were graded using the scoring system adapted from a published study (Libman et al., 2008). The score was designated from 1+ to 4+ as follows: 1+ represents 1-5 organisms/coverslip; 2+ represents 6-20 organisms/coverslip; 3+ represents ≥1 organisms per low-power field (100X magnification); 4+ represents ≥1 organisms per high-power field (400X magnification). After evaluating both slides, the highest score was recorded.

Blood parasite detection in this study was focused on Haemosporidian parasites (*Plasmodium*, *Haemoproteus* , and *Leucocytozoon*), which have been widely reported in both wild and domestic birds, causing Avian malaria. Calculation for Haemosporidian density (%parasitemia) was assigned in the study according to the Centers for Disease Control and Prevention (CDC) and World Health Organization (WHO) diagnostic procedures of blood specimen (CDC, 2016; World Health et al., 2015). Haemosporidian density was quantified by counting the affected red blood cells (RBCs) among 500-2,000 red blood cells and expressed the results as %parasitemia.

$$\%\text{parasitemia} = (\text{parasitized RBCs} \div \text{total RBCs}) \times 100$$

Statistical Analyses

All statistical analyses were carried out using R statistical software (RStudio, version 2022.12.0+353). The data set from both natural and treated breeding colonies including scale mass index, body condition score, brood size, infection, parasite prevalence, and infection severity according to the aforementioned grading method were used in the analyses. Besides sample groups classified by colony type, additional classification was added using infection status as a criterion. Birds that were infected by at least one pathogen were considered as “infected group” while the population that

doi:10.6342/NTU202302673

showed all negative (absent external parasite, absent helminth, protozoa = 0, spirochete = 0, blood parasite = 0), was considered as “naive group”. Physical fitness and reproductive performance were also compared between the infected and naive groups as well.

Each chick stage (egg, hatchling, sheath, fledgling) observed from both treated and natural colony types was calculated and presented in average number per nest to compare the trend of chick development between colony types as suggested in previous studies of synchronous breeding (Boland, 2004; 袁孝維 et al., 2003).

Prevalence, a proportion of infected bee-eater adults in a given time period, of each pathogenic organism was shown as a percentage of infected birds against the whole collected samples with a 90% confidence interval. Comparison of each parasite prevalence between two breeding colony types was performed using Pearson’s Chi-Square test unless one of the observation sizes is below five, Fisher’s Exact test was used instead.

Scale mass index was put into the analysis despite the fact that the body condition score was already assessed. This reassessment was to eliminate human error and bias when evaluating the bird’s body condition score since the criteria of each score were prone to be qualitative without a clear numerical cut-off. In general, the evaluator often used his/her own experience to determine the score. Mean scale mass index and body condition score, representing an animal's physical fitness, and average brood size, representing reproductive performance, were calculated with standard deviation.

Mann-Whitney U test was applied to test whether there was a difference in any physical fitness and reproductive performance indices between those natural and treated colonies using $p<0.05$ as a cut-off. The difference between infected and naive groups was

doi:10.6342/NTU202302673

also tested to affirm if parasite infection would alter bird physical fitness and reproductive performance or not.

A generalized linear mixed model from package glmmTMB was used to determine the best fitting model explaining the influence of any parasite infection (external parasite, helminth, protozoa, spirochete, and blood parasite) on scale mass index, body condition score, and brood size whereas the location of each single colony was set as random intercept (pathogen+(1 | site). Infection status and grade were used as the independent predictor variable. The first model (mSMI) determined whether infection impacts a scale mass index response whereas the second (mBCS) and third (mBR) determined whether the infection impacts bird body condition score and brood size respectively. Parasite predictors were used in each aforementioned model with five levels (single parasite infection, two parasites co-infection, three parasites co-infection, four parasites co-infection, and five parasites co-infection).

The first (mSMI) model started with the first level. The second level and beyond (another parasite predictor added, one at a time) will be formed to see the influence of co-infection if only the p-value of the previous level is significant ($p<0.05$). Otherwise, a deeper-level model will not be run. The second (mBCS) and third (mBR) models to determine the impact of infection to scale mass index and brood size followed the same pattern. The family of distribution applied in all possible models estimating scale mass index, body condition score, and brood size outcome were Gaussian, Gamma, and Negative binomial respectively.

For each model among the same level, model selection was performed using Akaike's information criterion corrected for small sample size (AICc) from package AICcmodavg in R. Only models with significant predictors which $\Delta AICc \leq 2$ compared

doi:10.6342/NTU202302673

to the best fitting model will be considered to support the data (Burnham & Anderson, 2002; Symonds & Moussalli, 2011).

As physical fitness could also affect the health and reproductive outcome (Peig & Green, 2009; Pigeault et al., 2019), both SMI and BCS were added as predictors in the generalized linear mixed model to find whether any of the body condition indices could affect the brood size using the same model selection criteria.

doi:10.6342/NTU202302673

Results

Nest status

A survey of the total nest count in Kinmen island was conducted for two consecutive weeks from the end of June to early of July 2022. A histogram of initial nest status was created to reduce the discrepancy of reproductive performance data. The first period was between June 22nd - 27th when the surveys were conducted in natural breeding colonies followed by the second period of July 2nd - 5th with all colonies observed being treated colonies.

The average number per nest for each nestling status observed in the natural colonies was 2.48 eggs, 1.33 hatchlings, 0.34 sheaths, and 0.07 fledglings. For the treated colonies, the average number of each status was 0.88 eggs, 0.74 hatchlings, 1.11 sheaths, and 0.48 fledglings per nest accordingly (Figure 1, page 61). During the catch, no bird showed signs of severe breathing complications (shallow breathing or mouth gaping), anemia, or dehydration during physical examination.

Comparison of parasite prevalence between two colony types

The prevalence of each pathogen infected in natural and treated colonies population was calculated separately. The 90% confidence interval (CI) was calculated in this study due to the low prevalence of some parasites. In natural breeding colonies population, the highest to lowest prevalence observed were protozoa (44.74%, CI = 31.47 - 58.01, n = 38), external parasite (24.39%, CI = 13.35 - 35.42, n = 41), blood parasite (9.76%, CI = 2.14 - 17.38, n = 41) followed by helminth and spirochete at the same proportion of 7.89% (CI = 0.70 - 15.08, n = 38).

doi:10.6342/NTU202302673

Treated colonies prevalence ranked from highest to lowest were external parasite (31.25%, CI = 23.47 - 39.03, n = 96), protozoa (15.85%, CI = 9.22 - 22.48, n = 82), spirochete (4.88%, CI = 0.97 - 8.79, n = 82), blood parasite (4.17%, CI = 0.81 - 7.53, n = 96) and helminth (1.22%, CI = -0.77 - 3.21, n =82) respectively. Only external parasite detected in natural colonies was lower whereas other pathogen prevalences were higher in the treated colonies (Figure 2, page 62).

All pathogens prevalence observed in both colony types were not significantly different except for fecal protozoa infection where the natural colonies had a higher prevalence than the treated colonies (df = 1, p = 0.0015). The summary of parasite prevalence and the p-value of each is shown in Table 3 (see page 73).

Detected parasites and grading

Chewing lice (Suborder Amblycera, n = 30) and louse flies (Genus Hippobosca, n = 2) were identified under microscopic examination from treated breeding colonies while only chewing lice were presented on the bee-eater's feathers in natural colonies. Several parasitic mites (suspected Genus Dermanyssus) and chewing lice were detected in sand samples collected from old nests. Three and one adult cestode (tapeworm) were detected in natural and treated colonies population respectively. One fecal sample from a natural colony (TPN) also contained cestode eggs with hatching hexacanth larvae.

Protozoa infection severity, when excluding negative results, ranged from grade 1+ to 4+. Modal, as known as the most frequent infection severity of protozoa was grade 1+ (1-5 organisms per coverslip) in both natural (8 of 38 individuals) and treated colonies (9 of 81 individuals). Unidentified flagellated protozoa, suspected of Giardia, and protozoa cysts were detected in both populations. Spirochete bacteria infection severity ranged from grade 1+ to 3+ in natural colonies where there was only 1 occurrence

doi:10.6342/NTU202302673

observed in each grade. Spirochete infection severity in treated colonies showed wider distribution from grade 1+ to 4+ where the modal infection severity was grade 1+ (2 of 81 individuals). Co-infection of fecal protozoa and spirochete was also observed in three birds, all from natural colonies (n = 2, FS; n = 1, TPS).

Eight blue-tailed bee-eaters were found infected by Haemosporidian parasites which all were suspected to be *Plasmodium spp*. gametocytes. Four of them resided in treated colonies where the most common infected birds were caught from Youth Farm (YFL). The number of Haemosporidian parasites was counted among 2,000 red blood cells and quantified into percentages of parasitemia (%parasitemia). Minimum and maximum blood parasite counts were 1 and 16 parasitized RBCs per 2,000 RBCs (%parasitemia = 0.05% - 0.8%, mean = 0.28%). The average %parasitemia in natural and treated colony types were 0.29% and 0.46% accordingly. All pathogens detected from blue-tailed bee-eater fecal and blood samples were shown in Figure 3 (page 63).

Comparison of SMI, BCS, and brood size according to colony type

The minimum and maximum SMI of birds from natural colonies were 31.51 and 43.57 grams. The minimum and maximum SMI of the treated colonies population was slightly higher, ranging from 31.77 to 45.60 grams respectively. However, natural colonies had a higher mean SMI of 38.34 ±2.95 grams (n = 40) compared to the treated colonies' SMI of 36.56 ± 2.64 grams (n = 96) (Figure 4, page 64). The range of bird body condition score (BCS) evaluated from both breeding colonies was 2.0 - 3.5 in natural colonies while the treated colonies range was lower of 1.5 - 3.0. Mean and standard deviation BCS of birds residing in natural and treated colonies were 2.53 ± 0.46 (n = 39)

doi:10.6342/NTU202302673

and 2.31 ±0.35 (n = 83) respectively (Figure 5, page 65). Both populations of BCS were considered to be slightly thin.

For the reproductive performance, only brood size (total number of eggs, hatchlings, sheaths, or fledglings) was counted and included in data analyses since any interruption to the chicks could create more risk of parents abandoning the nests. The least amount of brood size seen in natural colonies was the nest with two eggs in Tianpu south (TPS) colony. In the treated colonies, a nest with one hatchling and another with one fledgling was found in Youth Farm (YFL). The maximum amount of brood size observed in natural colonies was seven in total including six hatchlings and one egg from Fengshang (FS). The maximum brood size observed from treated colonies was six in total including five fledglings and one sheath. The average brood size observed in natural and treated colonies was 4.37 ±1.09 (n = 41) and 3.20 ±1.08 (n = 41) chicks in total accordingly (Figure 6, page 66).

The average SMI, BCS, and brood size of those from natural breeding colonies were significantly higher than the treated colonies (p = 0.00071, 0.02287, 0.0000104 respectively)

Comparison of SMI, BCS, and brood size according to infection status

Previous studies indicated that many disease infections could alter the body condition of birds, more specifically poorer body condition. The bee-eater population in Kinmen island was divided into two groups regardless of nest location and colony type including 1) the infected group in which one or more parasites were detected, and 2) the naive group in which none of the parasites was detected in any sample of an individual. The SMI, BCS, and brood size were compared between the two groups. The SMI of the

doi:10.6342/NTU202302673

infected group ranged from 31.51 to 43.57 grams and the naive group ranged from 31.77 to 45.60 grams. The average SMI of infected birds (37.50 ± 3.27, n = 61) was slightly higher than the naive birds (36.89 ± 2.52, n = 58).

BCS evaluated from both groups ranged from 1.5 to 3.5. A compared result of average BCS followed the same result as SMI where the infected (2.44 ± 0.38, n = 56) was also higher than the naive group (2.36 ± 0.43, n = 50). For the reproductive performance, the infected birds also had larger average brood size (3.98 ± 1.25, n = 48) compared to the naive group (3.69 ± 1.16, n = 26) (Figure 7-9, page 67-69). However, there were no significant differences between SMI, BCS, and brood size between infected and naive groups (Table 4, page 74).

Influence of infection on physical fitness

Physical fitness indicators in this study were comprised of the scale mass index (SMI) and body condition score (BCS). Among all the first-level models' evaluations which examine any single organism influencing the SMI, the external parasite was the best fitting prediction model (AICc = 585.11, p = 0.204). However, none of the first-level models showed statistical significance and the best model AICc weight indicating predictive power was quite low (W = 0.30). Therefore, a deeper level investigation by adding co-infection into models was omitted. In this sense, bee-eater SMI was neither influenced by any organisms observed during June - July 2022 nor the co-infection of two or more organisms in one adult played a significant role on bee-eater SMI.

There was also no significant predictor explaining the impact of parasite infection on bird BCS. Testing all the first-level models found that the external parasite was also the best fitting model (AICc = 118.52, p = 0.75) with even lower predictive power (W =

doi:10.6342/NTU202302673

0.22). However, using colony type alone as a predictor showed a significant influence on BCS (AICc = 116.3, p = 0.00632).

Influence of infection and physical fitness on reproductive performance

Model using helminth infection as an indicator to brood size was removed due to the 0% prevalence in FS, OCN, TPS, CC, and CC sites. As the data did not contain enough information causing the over-parameterized model, therefore, the model could not estimate the parameters reliably (Table 5, page 75). The most suitable first-level model was one using spirochete infection as a predictor (AICc = 269.08, p = 0.629). Yet none of the prediction models showed significant p-value influencing the brood size. Only the model using colony type alone could be considered as a good predictor of brood size (AICc = 231.8, p = 0.000531). Thus bee-eaters reproductive performance using brood size as a criterion was not affected by any pathogen infection as well as the co-infection of two or more pathogenic organisms (Table 6, page 76).

When investigating further predictors related to body condition which might also influence bee-eater reproductive performance, neither SMI nor BCS had a significant influence on brood size (AICc = 264.4, p = 0.172, and AICc = 270.1, p = 0.244 respectively).

doi:10.6342/NTU202302673

Discussion

Nest status between natural and treated colonies

The total nest count, including active nests which contain any nestling stage and non-active (abandoned or already fledged) nests, of treated colonies was around 4 times higher than the natural colonies. The majority of nestling stages occupying the nests in natural colonies were eggs and hatchlings, in contrast to the treated colonies where most nests were occupied by sheaths and fledglings. Some nestlings in treated colonies had already fledged as they showed signs of pre-existing active nests such as remnants of insect parts and dried feces (Figure 1, page 61).

The finding could be implied that the blue-tailed bee-eaters that arrived at Kinmen island earlier prefer the treated colonies and in consequence, laid eggs prior to the natural colonies. This finding could be explained by the characteristics of treated colonies where there was less vegetation covered. Dense vegetation has two important disadvantages. It can impede the bird's ability to excavate its nest, and it masks the bird's visibility of predators which can reduce its ability to perform mobbing behavior (Wang et al., 2009; Yuan et al., 2006). Even though birds living in larger colonies would have to compete for food resources, the benefit of predator detection by the community had won over.

Furthermore, several studies found that burrowing birds preferred to build their nests along the upper margin of the slope followed by the lower margin later on not too hard or too soft soil slope. This particular choice was to decrease the risk of predation by living in closer proximity to the ground and risk of nest collapse respectively (Smalley et al., 2013; 林昀萱, 2022). These findings were in congruence with the characteristics of present colonies in Kinmen island where the majority of active nests in all treated colonies located further from the ground, believed to put more difficulty to snakes and mice to

doi:10.6342/NTU202302673

access. Site fidelity was also mentioned to explain the nest site decision of bee-eaters. Site fidelity was reported in a past study conducted on Kinmen island where birds were more likely to reuse the same colony in consecutive years due to their past reproductive success (蔡佩妤, 2007). Nest re-occupation was also reported in European bee-eaters therefore reducing time and saving energy (Brust et al., 2015).

The limitation of nest status survey

The nest survey procedure had limitations which could lead to failure to meet the accurate data analyses due to asynchronous observation time therefore hatching time. The first period of the survey (June 22nd - 27th) only contained the natural breeding sites while only treated breeding sites were observed during the second period (July 2nd - 5th). A seven-day prediction of the nestling stage could be a useful approach, yet it might not be practical according to previous studies of reproductive biology in bee-eaters. Despite the known mean hatching till fledging period being 20 - 24 days (袁孝維 et al., 2003), it cannot be assumed that the duration of each stage was divided equally. Another study suggested a photographic guide to differentiate each nestling stage which needs approximately 12 days to distinctively identify each nestling stage (Costa et al., 2020). In addition, individual nestling development could be different in each breeding site or even each nest due to the difference in numbers of helpers, food availability, and the number of nestlings per nest added to sibling competition (Arbeiter et al., 2016; Lessells & Avery, 1989). Therefore, the chick status, despite tracing back to seven days prior, could not be accurately predicted. In this sense, it is still uncertain whether the later stage of nestlings observed in treated colonies was a product of early arrival birds or observation time. Data

doi:10.6342/NTU202302673

collection with observation time conflicts could be improved by putting more labor into the nest status survey within a shorter time frame to reduce the data collection errors.

Comparison of parasite prevalence

Previous studies indicated that higher density breeding grounds were prone to have a higher risk of infection, therefore poorer body condition as well as breeding performance are expected in treated colonies. Unexpectedly, the prevalence of all pathogens in treated colonies, except for external parasites, was lower than in the natural colonies. Only intestinal protozoa infection in natural colonies was significantly higher than the treated colonies while the prevalence of other pathogens showed no sign of difference. The finding was in accordance with a study of Buggy Creek virus (BCRV) in Cliff swallow nestlings (*Petrochelidon pyrrhonota*). The authors found that the prevalence of the virus increased where the colony size was larger, however, the prevalence decreased significantly if the number of individual presence increased, as known as the "Dilution effect" (O'Brien & Brown, 2011).

The dilution effect

The dilution effect occurs in the high diversity ecosystem where species have a wide range of susceptibility to pathogen infection. This effect limits the disease spread and lessens epidemics via several mechanisms. One of them is when the non-host species such as predators or competitors may dilute the infection directly and indirectly (Khalil et al., 2016). Though previous studies indicated that the magnitude of the dilution effect is likely to depend on the frequency of exposure rather than the host density (Civitello et al., 2015), disease surveillance of non-host species around bee-eater colonies should not

doi:10.6342/NTU202302673

be disregarded. This could also be a possible explanation for why the prevalence of intestinal worms, spirochetes, and blood parasites was low and insignificantly different.

Parasitic mites and chewing lice were detected in the soil collected from abandoned nests. Despite universal knowledge that external parasites such as fowl mites or feather lice are common in wild birds, the prevalence of parasitic insects found in blue-tailed bee-eaters was low, without significant difference between the two colony types. A previous study indicated that several parasitic arthropods were detected in active and old European bee-eater nests where they were reused by other species (Casas-Crivillé & Valera, 2005). In the multi-host scenario, several parasites can be a generalist rather than a specialist. When a suitable host is scarce, the alternative hosts are targeted strongly dependent on the availability at that moment (Manzoli et al., 2021). Thus the plasticity of host selection may reduce an infection rate.

Host behavior and physical characteristics

The main external parasite found in blue-tailed bee-eater bodies was Ambleceran lice. This arthropod feeds on dead skin and feathers resulting in irritation and stress to the host. Most host reacts to the infestation by preening and scratching behavior, which in a previous experimental study showed that the prevalence of lice in preening birds could be decreased by 50% (Sarah & Dale, 2023). Somehow, excessive preening behavior costs negative effects on time and energy that should be invested in other activities such as growth and reproduction (Hoi et al., 2012; Rassouli et al., 2016).

Physical characteristics of host species have diversified the parasite-host relationship as well as the ability to co-evolve. A study among the bird community in New Guinea found that bird species with curved bills encountered a significantly lower number of mites compared to straight billed species (Bodawatta et al., 2022). The curved

doi:10.6342/NTU202302673

bills may improve the ability to remove mites during preening. Blue-tailed bee-eater may be able to partially disrupt the attachment of the feather lice therefore its prevalence was lower than expected.

Parasite infection mechanism

Despite the distinctively higher fecal protozoa prevalence in natural colonies, this parameter alone could not implicate whether treated colonies were a better suitable breeding ground for blue-tailed bee-eaters. This finding could be explained by its nature of transmission and structure. Fecal protozoans are transmitted through the fecal-oral route, one of the most common and easiest direct transmissions due to their ability to transfer the pathogen between the primary host without the intermediate host or vector (Schuster & Krone, 2016). The source of infection includes the contaminated environment and direct contact with infected animals should also be considered. Contaminated water bodies around breeding colonies are suspected to be a key transmission source of waterborne parasites such as Giardia, as well as other remnant protozoan cysts in the nests due to its thick, environmentally resistant wall (Hogan, 2012; Suh et al., 2015; Yabsley, 2008). Thus a significant protozoan prevalence comparing between colony types might be arbitrary.

Natural ponds and reservoirs around the breeding colonies, especially the locations that bee-eater populations use as water sources should also be inspected. Regardless of colony types, two breeding colonies are situated near each other (FS and CC, 900m in displacement) surrounded by several reservoirs and agriculture ponds where they may share similar origins. In following suit, the prevalence of fecal protozoa detected in FS and CC were 60% and 75% respectively, this could be implied that there was a

doi:10.6342/NTU202302673

possibility of overlapping foraging areas between these two breeding colonies, thus sharing the same water resources (Figure 10, page 70).

The species of all parasites detected in bee-eater samples could not be clearly identified by the limitation of microscopic method, due to its low sensitivities and specificities. Fecal floatation and fecal sedimentation are recommended to detect and identify intestinal parasites, particularly helminth and protozoan species. However, due to an insufficient amount of feces collected, these detection methods were impossible to perform, therefore affecting the interpretation and underestimating the prevalence where false negative samples might have occurred. Further investigation using more advanced diagnostic technologies such as immunodiagnostic methods or nucleic-acid-based detection techniques would enhance the accuracy and reliability of parasite detection and identification (Fitri et al., 2022; McHardy et al., 2014).

Another factor needed to be considered is the nature of infectious pathogens. Each pathogen has different characteristics (e.g. its definitive host, incubation period, and transmission rate) which alter the host physiology and by all means, affect the prevalence differently. Therefore, the colony size and density alone may not be reliable parameters to predict the likelihood of disease infection rate in the population.

Considering on a larger scale where there is more than one host available, the biodiversity-disease relationships are nonlinear. Differences in parasite infections between two colony types may result from numerous ecological factors including differences in distributions of parasite-transmitting vectors and subsequent host exposure, the spatial overlap between host and vectors, physiological differences in disease resistance of individual host, or levels of sociality of each colony (Bobby Fokidis et al., 2008; Halliday & Rohr, 2019). Additional multifactorial research such as environmental

doi:10.6342/NTU202302673

examination and organism identification could help map out the transmission origin and clarify disease prevalence among breeding colonies. Understanding the infection patterns of each pathogen detected in the samples will prevent inconclusive results in the future.

Comparison of body condition and reproductive performance

Scale mass index (SMI), body condition score (BCS), and brood size of birds residing in natural colonies were significantly higher than those of the treated colonies. Although the results were in congruence with the second hypothesis, they did not match with the first one presupposing that the treated colonies should have higher parasite prevalence. Therefore, the body condition and reproductive performance of bee-eaters should not be determined by colony size, but arrival time and reserved energy allocation might provide more insight.

Bird migration strategies

Arrival timing of migratory birds might be a key explaining the findings. Studies found that birds who experienced a better environment, where they gain relatively better body condition, had more survival rate, arrived at the breeding ground earlier, and were able to choose their favorable breeding areas (Alves et al., 2013; Dossman et al., 2023; Duijns et al., 2017). Fitness inequalities may play an important role in migration timing and egg laying strategy as well as other factors.

Non-breeding grounds or places of origin are also needed to be considered where they might affect the migration strategy. Early arrival birds, as known as income migrators, are believed to migrate from nearer non-breeding locations, then sprint all the way to the breeding grounds where they can advantageously access better quality and quantity food resources, thus laying eggs earlier. In contrast to the late arrivers or capital

doi:10.6342/NTU202302673

migrators which deposit energy from their non-breeding ground or along the migration route (Alerstam, 2006; Klaassen, 2003). Moreover, either because of greater distance to the breeding grounds or other complications interfere with the migration timing such as adverse effects of infection (Ágh et al., 2022; Ágh et al., 2019), some migratory birds compensate for their late arrival by speeding up their migration rate or shortening the incubation period to compete with resources access. However, there is a trade-off of traveling at a faster rate, the survival rate may decrease (Cuevas et al., 2021; Dossman et al., 2023). In this manner, better body condition should be observed in treated colonies regardless of infection status.

This contradiction could be explained by the energy management strategy of the parents. During the pre-breeding and breeding period, migratory birds have to allocate their energy wisely to optimize highest reproductive success with less health compromise. According to the nest status observed in natural colonies where the majority of nests were in early stages, both body condition score and body mass were slightly higher than the treated colonies birds with later life stage nestlings. Despite one parent is required to stay inside the burrow while its counterpart is in charge of finding food, the energy investment of the counterpart is still lower compared to the treated colonies birds which had to feed the fast-growing nestlings. Though both parents can leave the nest, rapid growth rate and higher food demand might somehow put an energetic constraint on bee-eater parents. Therefore birds residing in natural colonies tended to have better body condition.

Nonetheless, body condition score evaluation could be primed due to the observer's bias. Recaptured birds' BCS and weight were re-measured and recorded in the new datasheet without prior information from the previous catch. Most of the recaptures showed decreasing in BCS and body mass over time (Table 7, page 78).

doi:10.6342/NTU202302673

Energy management and feeding frequency in breeding pairs are also influenced by various factors both at the individual level and community level. A study in tree swallow indicated that a decrease in an individual's foraging efficacy could lead to greater loss of body mass due to limited energy allocation between its own condition and the nestlings (Ardia & Clotfelter, 2006). Food availability as well as habitat disturbance not only alters the foraging behavior, it also affects the bird body condition (Cox & Cresswell, 2014; Strong & Sherry, 2000; Yang et al., 2015). It is also possible that while birds choose to breed in more populated treated colonies to fend off the predators, competition for food can be challenging for both parents and their chicks. Nevertheless, the body condition score from both colony types was considerably indifferent (BCS = 2.53 ± 0.46 in natural colonies and 2.31 ±0.35 in treated colonies). This may be due to the presence of non-breeding helpers alleviating the workload of breeding couples, or higher prey abundance in treated colonies.

Comparison of reproductive performance

Reproductive performance in this study was determined by the number of eggs and nestlings regardless of the growth stages. It determines the initial brood size which the birds could lay after completion of the nests (Boland, 2004). This study found a significantly higher average brood size in natural colonies compared to the treated (4.37 ±1.09 and 3.20 ±1.08 respectively).

It is common to see less nestling in the treated colonies due to the selective pressure from unpredictable environments including having predators around or food scarcity may alter the parent's behavior to feed the stronger chicks prior to the weaker ones (Caro et al., 2016). In consequence, poorer condition nestlings could not survive

doi:10.6342/NTU202302673

eventually. Furthermore, as reported in a previous study conducted in Kinmen, the larger breeding colonies also suffered from avian predators hunting for the eggs and small hatchlings which could alter the reproductive strategies (林昀萱, 2022). Parents decrease their clutch size and feeding rate if there was a higher risk of predation around their nests to avoid costs associated with reproductive success (Dillon & Conway, 2017; Fontaine & Martin, 2006).

Influence of infection on physical fitness (GLMM)

The data set was re-evaluated by categorizing all bird samples according to their infection status, in which one or more pathogens detected in a sample were treated as infected, and the sample without any infection was treated as naive. The purpose of re-categorizing these samples was to review if parasitism has an impact on bee-eaters' fitness.

In contrast to the original hypothesis, the SMI, BCS, and brood size of infected birds were slightly higher than the naive birds. However, all three parameters were not statistically significant between the infected birds and the naive birds. Therefore, the outcome of poorer fitness in treated colonies might not cause by the infection alone. In addition, GLMM analysis resulted in no correlation of disease prevalence influencing physical fitness (SMI, BCS) as well as influencing the reproductive performance in blue-tailed bee-eaters observed in Kinmen island during summer 2022.

These findings were in concordance with previous studies indicating that there was no relationship between infection status and body condition, body size, or fat measures (Ágh et al., 2019; Bobby Fokidis et al., 2008; Cornelius et al., 2014; Granthon & Williams, 2017; Kelly et al., 2020; Oniki-Willis et al., 2023). One study showed that

doi:10.6342/NTU202302673

only a heavy infestation of chewing lice had effects on European bee-eater body mass which could be due to loss of feathers (Hoi et al., 2012).

Selective disappearance

Since blue-tailed bee-eaters are migratory birds, the source and time of disease exposure are unknown. The infected birds could come from further non-breeding grounds with possibly higher disease prevalence. Consequentially the infection might either unfavorably affect the migration timing or migration speed rather than the body condition (Ágh et al., 2019). Selective disappearance may explain the indifference to body condition between the infected and naive groups.

In the case of avian malaria, the high mortality chance often occurs during the high parasitemia stage. This stage only last in a pattern of acute and short periods of time. If an individual could survive the parasitemia period, the bird will stay in chronic infection where the parasite will affect lower fitness cost. Hence infected birds that could not survive or alter their migration strategies (refuse or delay migration) that season would not be observed in breeding grounds (Jimenez-Penuela et al., 2019). Infected birds may show a lower variation in BCS which was also in accordance with the result of this study (Figure 8, page 68). The population's maximum %parasitemia was shown to be only 0.8% and was considered to be a chronic infection due to a very low amount of defective red blood cells seen in the microscopic field. Several studies discussed that chronic infection might not be pathogenic enough to impact the overall health or some host species are able to evolve along with the parasites and become resistant to them. Thus infection had minimal effects on the host's health and body condition (Cornelius et al., 2014; Granthon & Williams, 2017).

doi:10.6342/NTU202302673

Influence of infection and physical fitness on reproductive performance (GLMM)

Neither infection nor body condition was a suitable predictor of bee-eater brood size. According to the previous study of the bee-eater population in Kinmen, colony size had no significant correlation with breeding success as all breeding colonies observed showed more than 90% success rate (林昀萱, 2022). It could be implied in this study that even though both SMI and BCS of birds from natural colonies appeared to be significantly higher than those treated colonies, physical fitness alone might not have a direct effect on the brood size.

Ecological factors once again play an important role in influencing the reproductive outcome. As mentioned before, food availability is a classic explanation of the breeding strategy, thus affecting reproductive performance. Less food availability due to declining prey abundance or increasing competitors partially result in females laying smaller clutch size as a trade-off (Decker et al., 2012; Tortosa et al., 2003). The aspect of condition-dependent optimization, in which a female needs more time to gain sufficient nutrients to lay additional eggs to increase its reproductive success (Reséndiz-Infante & Gauthier, 2020), was plausible, especially in breeding sites with lower prey abundance.

Bird's natural variation

Although some studies indicated that co-infection and both infected parents did a better job raising their nestlings resulting in higher reproductive success, these findings might be due to biased sampling rather than the direct effect of infection on reproductive success. In contrast with reproductive performance, extreme infection can cause a declining probability of survival. Only high-functioning individuals could migrate and breed despite infection (Pigeault et al., 2018; Pigeault et al., 2019; Zylberberg et al., 2015).

doi:10.6342/NTU202302673

Age and individual quality also influence clutch size where most studies found that older, experienced females invested more in egg reproduction as well as bird heredity as an important key of clutch traits (Decker et al., 2012; Postma & van Noordwijk, 2005; Wolc et al., 2019; Zylberberg et al., 2015). Age of males also played a role in reproductive success, let alone the individual's fertility, but the better parental care of older males also tripled the fledging rate compared to the sub-adult male in the same population (Pigeault et al., 2019).

Study limitation on monitoring reproductive performance and sample size

Due to time constraints and the vulnerability of parents abandoning their nests, there was not adequate data on other reproductive parameters indicating more precise breeding success such as hatching or fledging rate, nestling body condition as well as the changes of brood numbers through the whole summer where a chance of delayed extra eggs could be observed. Therefore, using brood size as the main measurement for reproductive performance may need to be reconsidered where bias by a changing condition through time could happen.

Another possible explanation for the failure to address the infection's impact on birds 'fitness and reproductive performance might be due to the sample size. Hedges' g effect size was calculated and shown in Table 4 (see page 74). The magnitudes of the difference between the SMI, BCS, and brood size of infected and naive bird groups were 0.20, 0.19, and 0.24 respectively. More bird samples could have been collected to enhance the statistical power. However, due to time constraints, more samples were not able to be obtained.

There is a missing linkage between physical fitness as well as infection status and reproductive performance observed in this study. Factors mentioned above could explain

doi:10.6342/NTU202302673

that several aspects besides physical fitness and infection status might also have an influence on reproductive outcomes.

doi:10.6342/NTU202302673

Conclusions

Considering the overall physical fitness during a summer survey in Kinmen island, though the bird average BCS of both colony types was slightly thin, it is still within an acceptable range for a breeding period due to the energy expense of raising chicks. External parasites, gastrointestinal parasites as well as blood parasite prevalence observed in both populations were lower than expected despite the significant difference in body condition and brood size between natural and treated colonies. It is inconclusive to accept the hypothesis that natural colonies contain superior qualities than the treated colonies. When investigating further if these indices affect the population fitness, there was no correlation of disease infection influencing bird body condition or reproductive performance. Lastly, there was no correlation between bird body condition impacting reproductive performance.

Without any serious health concerns detected in this population, the blue-tailed bee-eaters residing in Kinmen island were in good condition thus far. Human intervention by breeding grounds alteration did not have a critical impact on its population health and reproductive performance. However, the number of summer migrants coming to the island was gradually declined. Conservation attempt to sustain the blue-tailed bee-eater number requires more integrative data for a greater level of understanding of its population dynamics in Kinmen island.

There are a variety of interrelation trade-offs in migratory birds that influence their body condition, breeding strategies, and breeding grounds selection. Environment (climate change, food abundance, local competitors and predators, resources quality), flock structure (bird age, breeding:non-breeding ratio) of each breeding site as well as host and parasite traits and their relationship should be further investigated to find out the

doi:10.6342/NTU202302673

substantial drivers behind the physical fitness and reproductive outcomes between two colony types.

Field studies in wildlife are challenging where different methods used to evaluate body condition could alter the outcomes (Sánchez et al., 2018). Ecologists conducting wildlife research should consider not only the host-parasite biology, employing a longitudinal survey during the breeding period could be beneficial for understanding the relationship between parasite infection and the health of interested species.

doi:10.6342/NTU202302673

References

Ágh, N., Csörgő, T., & Szöllősi, E. (2022). Delay in arrival: lineage-specific influence of haemosporidians on autumn migration of European robins. *Parasitology Research*, *121*(10), 2831-2840. https://doi.org/10.1007/s00436-022-07621-5

Ágh, N., Piross, I. S., Majoros, G., Csorgo, T., & Szollosi, E. (2019). Malaria infection status of European Robins seems to associate with timing of autumn migration but not with actual condition. *Parasitology*, *146*(6), 814-820. https://doi.org/10.1017/S0031182018002184

Alerstam, T. (2006). Strategies for the transition to breeding in time-selected bird migration. *Ardea*, *94*, 347-357.

Alves, J. A., Gunnarsson, T. G., Hayhow, D. B., Appleton, G. F., Potts, P. M., Sutherland, W. J., & Gill, J. A. (2013). Costs, benefits, and fitness consequences of different migratory strategies. *Ecology*, *94*(1), 11-17. https://doi.org/https://doi.org/10.1890/12-0737.1

Arbeiter, S., Schulze, M., Tamm, P., & Hahn, S. (2016). Strong cascading effect of weather conditions on prey availability and annual breeding performance in European bee-eaters Merops apiaster. *Journal of Ornithology*, *157*(1), 155-163. https://doi.org/10.1007/s10336-015-1262-x

Ardia, D. R., & Clotfelter, E. D. (2006). Individual quality and age affect responses to an energetic constraint in a cavity-nesting bird. *Behavioral Ecology*, *18*(1), 259-266. https://doi.org/10.1093/beheco/arl078

Blas, J. (2015). Stress in Birds. In *Sturkie's Avian Physiology* (pp. 769-810). https://doi.org/10.1016/b978-0-12-407160-5.00033-6

doi:10.6342/NTU202302673

Bobby Fokidis, H., Greiner, E. C., & Deviche, P. (2008). Interspecific variation in avian blood parasites and haematology associated with urbanization in a desert habitat. *Journal of Avian Biology*, *39*(3), 300-310. https://doi.org/https://doi.org/10.1111/j.0908-8857.2008.04248.x

Bodawatta, K. H., Shriner, I., Pigott, S., Koane, B., Vinagre-Izquierdo, C., Rios, R. S., Jønsson, K. A., & Tori, W. P. (2022). Ecological factors driving the feather mite associations in tropical avian hosts. *Journal of Avian Biology*, *2022*(6). https://doi.org/10.1111/jav.02951

Boland, C. (2004). Breeding Biology of Rainbow Bee-Eaters (Merops ornatus): A Migratory, Colonial, Cooperative Bird. *The Auk*, *121*. https://doi.org/10.2307/4090318

Brown, C. R., & Brown, M. B. (2004). Empirical Measurement of Parasite Transmission between Groups in a Colonial Bird. *Ecology*, *85*(6), 1619-1626. https://doi.org/https://doi.org/10.1890/03-0206

Brust, V., Bastian, H. V., Bastian, A., & Schmoll, T. (2015). Determinants of between-year burrow re-occupation in a colony of the European bee-eater Merops apiaster. *Ecol Evol*, *5*(15), 3223-3230. https://doi.org/10.1002/ece3.1563

Burnham, K. P., & Anderson, D. R. (2002). Information and Likelihood Theory: A Basis for Model Selection and Inference. In K. P. Burnham & D. R. Anderson (Eds.), *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (pp. 49-97). Springer New York. https://doi.org/10.1007/978-0-387-22456-5_2

doi:10.6342/NTU202302673

Burton, E. J., Newnham, R., Bailey, S. J., & Alexander, L. G. (2014). Evaluation of a fast, objective tool for assessing body condition of budgerigars (Melopsittacus undulatus). *J Anim Physiol Anim Nutr (Berl)*, *98*(2), 223-227. https://doi.org/10.1111/jpn.12063

Caro, S. M., Griffin, A. S., Hinde, C. A., & West, S. A. (2016). Unpredictable environments lead to the evolution of parental neglect in birds. *Nature Communications*, *7*(1), 10985. https://doi.org/10.1038/ncomms10985

Casas-Crivillé, A., & Valera, F. (2005). The European bee-eater (Merops apiaster) as an ecosystem engineer in arid environments. *Journal of Arid Environments*, *60*(2), 227-238. https://doi.org/10.1016/j.jaridenv.2004.03.012

CDC. (2016). *Blood Specimens - Microscopic Examination*. https://www.cdc.gov/dpdx/diagnosticprocedures/blood/microexam.html

Chastel, O., Weimerskirch, H., & Jouventin, P. (1995). Influence of Body Condition on Reproductive Decision and Reproductive Success in the Blue Petrel. *The Auk*, *112*(4), 964-972. https://doi.org/10.2307/4089027

Civitello, D. J., Cohen, J., Fatima, H., Halstead, N. T., Liriano, J., McMahon, T. A., Ortega, C. N., Sauer, E. L., Sehgal, T., Young, S., & Rohr, J. R. (2015). Biodiversity inhibits parasites: Broad evidence for the dilution effect. *Proceedings of the National Academy of Sciences*, *112*(28), 8667-8671. https://doi.org/doi:10.1073/pnas.1506279112

Clark, N. F., & Taylor-Robinson, A. W. (2021). An Ecologically Framed Comparison of The Potential for Zoonotic Transmission of Non-Human and Human-Infecting Species of Malaria Parasite. *Yale J Biol Med*, *94*(2), 361-373.

doi:10.6342/NTU202302673

Clark, P., Boardman, W., & Raidal, S. (2009). Hemoparasites of birds. In *Atlas of Clinical Avian Hematology* (1st ed., pp. 129-130). Wiley-Blackwell.

Cornelius, E. A., Davis, A. K., & Altizer, S. A. (2014). How important are hemoparasites to migratory songbirds? Evaluating physiological measures and infection status in three neotropical migrants during stopover. *Physiol Biochem Zool*, *87*(5), 719-728. https://doi.org/10.1086/677541

Costa, J. S., Rocha, A. D., Correia, R. A., & Alves, J. A. (2020). Developing and validating a nestling photographic aging guide for cavity-nesting birds: an example with the European Bee-eater (Merops apiaster). *Avian Research*, *11*(1). https://doi.org/10.1186/s40657-020-0188-z

Côté, I. M., & Poulinb, R. (1995). Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology*, *6*(2), 159-165. https://doi.org/10.1093/beheco/6.2.159

Cox, D. T. C., & Cresswell, W. (2014). Mass gained during breeding positively correlates with adult survival because both reflect life history adaptation to seasonal food availability. *Oecologia*, *174*(4), 1197-1204. https://doi.org/10.1007/s00442-013-2859-5

Cuevas, E., Orellana-Peñailillo, C., Botero-Delgadillo, E., Espíndola-Hernández, P., Vásquez, R. A., & Quirici, V. (2021). Influence of the haemosporidian Leucocytozoon spp. over reproductive output in a wild Neotropical passerine, the Thorn-tailed Rayadito (Aphrastura spinicauda). *Ibis*, *163*(3), 948-961. https://doi.org/10.1111/ibi.12934

doi:10.6342/NTU202302673

Cuthbert, R. J., Cooper, J., & Ryan, P. G. (2014). Population trends and breeding success of albatrosses and giant petrels at Gough Island in the face of at-sea and on-land threats. *Antarctic Science*, *26*(2), 163-171. https://doi.org/10.1017/S0954102013000424

da Silva Rodrigues, R., de Souza Penha, V. A., Miwa, R. Y., Branco, J. O., & Junior, O. M. (2021). Stress and Body Condition Predict Haemosporidian Parasitaemia in Birds from Cerrado, Southeastern Brazil. *Ardea*, *109*(2), 175-183, 179. https://doi.org/10.5253/arde.v109i3.a7

Decker, K. L., Conway, C. J., & Fontaine, J. J. (2012). Nest predation, food, and female age explain seasonal declines in clutch size. *Evolutionary Ecology*, *26*(3), 683-699. https://doi.org/10.1007/s10682-011-9521-7

Dillon, K. G., & Conway, C. J. (2017). Nest predation risk explains variation in avian clutch size. *Behavioral Ecology*, *29*(2), 301-311. https://doi.org/10.1093/beheco/arx130

Doneley, R. (2016). The Clinical Examination. In *Avian Medicine* (pp. 49-72). https://doi.org/10.1016/b978-0-7234-3832-8.00005-5

Dossman, B. C., Rodewald, A. D., Studds, C. E., & Marra, P. P. (2023). Migratory birds with delayed spring departure migrate faster but pay the costs. *Ecology*, *104*(2), e3938. https://doi.org/https://doi.org/10.1002/ecy.3938

Duijns, S., Niles, L. J., Dey, A., Aubry, Y., Friis, C., Koch, S., Anderson, A. M., & Smith, P. A. (2017). Body condition explains migratory performance of a long-distance migrant. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1866), 20171374. https://doi.org/10.1098/rspb.2017.1374

doi:10.6342/NTU202302673

Fitri, L. E., Candradikusuma, D., Setia, Y. D., Wibawa, P. A., Iskandar, A., Winaris, N., & Pawestri, A. R. (2022). Diagnostic Methods of Common Intestinal Protozoa: Current and Future Immunological and Molecular Methods. *Tropical Medicine and Infectious Disease*, *7*(10), 253. https://www.mdpi.com/2414-6366/7/10/253

Fontaine, J. J., & Martin, T. E. (2006). Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters*, *9*(4), 428-434. https://doi.org/https://doi.org/10.1111/j.1461-0248.2006.00892.x

Gameiro, J., Veiga, J., Valera, F., Palmeirim, J. M., & Catry, I. (2021). Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies. *Parasitology*, *148*(8), 904-912. https://doi.org/10.1017/S0031182021000470

Gosler, A. G. (1991). On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit (Parus major). *Bird Study*, *38*(1), 1-9. https://doi.org/10.1080/00063659109477061

Granthon, C., & Williams, D. A. (2017). Avian Malaria, Body Condition, and Blood Parameters In Four Species of Songbirds. *The Wilson Journal of Ornithology*, *129*(3), 492-508, 417. https://doi.org/10.1676/16-060.1

Halliday, F. W., & Rohr, J. R. (2019). Measuring the shape of the biodiversity-disease relationship across systems reveals new findings and key gaps. *Nature Communications*, *10*(1), 5032. https://doi.org/10.1038/s41467-019-13049-w

Hayes, C. D., Hayes, T. I., McClure, C. J. W., Quiroga, M., Thorstrom, R. K., & Anderson, D. L. (2018). Native parasitic nest fly impacts reproductive success of an island-endemic host. *Animal Conservation*, *22*(2), 157-164. https://doi.org/10.1111/acv.12449

doi:10.6342/NTU202302673

Hicks, O., Green, J. A., Daunt, F., Cunningham, E. J. A., Newell, M., Butler, A., & Burthe, S. J. (2019). Sublethal effects of natural parasitism act through maternal, but not paternal, reproductive success in a wild population. *Ecology*, *100*(8), e02772. https://doi.org/https://doi.org/10.1002/ecy.2772

Hogan, J. N. (2012). *Epidemiology of Fecal Protozoa at the Human, Animal, and Environmental Interface* University of California Davis]. https://escholarship.org/uc/item/0sx0n5tt

Hoi, H., Darolová, A., Krištofík, J., & Hoi, C. (2017). The effect of the ectoparasite Carnus hemapterus on immune defence, condition, and health of nestling European Bee-eaters. *Journal of Ornithology*, *159*(1), 291-302. https://doi.org/10.1007/s10336-017-1500-5

Hoi, H., Krištofík, J., Darolová, A., & Hoi, C. (2010). Are parasite intensity and related costs of the milichiid fly Carnus hemapterus related to host sociality? *Journal of Ornithology*, *151*(4), 907-913. https://doi.org/10.1007/s10336-010-0529-5

Hoi, H., KriŠTofÍK, J., DarolovÁ, A., & Hoi, C. (2012). Experimental evidence for costs due to chewing lice in the European bee-eater (Merops apiaster). *Parasitology*, *139*(1), 53-59. https://doi.org/10.1017/S0031182011001727

Ilgūnas, M., Bukauskaitė, D., Palinauskas, V., Iezhova, T. A., Dinhopl, N., Nedorost, N., Weissenbacher-Lang, C., Weissenböck, H., & Valkiūnas, G. (2016). Mortality and pathology in birds due to Plasmodium (Giovannolaia) homocircumflexum infection, with emphasis on the exoerythrocytic development of avian malaria parasites. *Malaria Journal*, *15*(1). https://doi.org/10.1186/s12936-016-1310-x

IUCN. (2016). *Blue-tailed Bee-eater*. https://www.iucnredlist.org/species/22683750/92998513

doi:10.6342/NTU202302673

Jimenez-Penuela, J., Ferraguti, M., Martinez-de la Puente, J., Soriguer, R., & Figuerola, J. (2019). Urbanization and blood parasite infections affect the body condition of wild birds. *Sci Total Environ*, *651*(Pt 2), 3015-3022. https://doi.org/10.1016/j.scitotenv.2018.10.203

Kaminski, M., Janiszewski, T., Indykiewicz, P., Nowakowski, J. J., Kowalski, J., Dulisz, B., & Minias, P. (2021). Density-dependence of nestling immune function and physiological condition in semi-precocial colonial bird: a cross-fostering experiment. *Front Zool*, *18*(1), 7. https://doi.org/10.1186/s12983-021-00388-y

Kelly, T. R., Rubin, B. D., MacDougall-Shackleton, S. A., & MacDougall-Shackleton, E. A. (2020). Experimental Malaria Infection Affects Songbirds' Nocturnal Migratory Activity. *Physiol Biochem Zool*, *93*(2), 97-110. https://doi.org/10.1086/707495

Khalil, H., Ecke, F., Evander, M., Magnusson, M., & Hörnfeldt, B. (2016). Declining ecosystem health and the dilution effect. *Scientific Reports*, *6*(1), 31314. https://doi.org/10.1038/srep31314

Klaassen, M. (2003, 2003//). Relationships Between Migration and Breeding Strategies in Arctic Breeding Birds. Avian Migration, Berlin, Heidelberg.

Krams, R., Krama, T., Elferts, D., Daukšte, J., Raibarte, P., Brūmelis, G., Dauškane, I., Strode, L., & Krams, I. A. (2022). High Blood Parasite Infection Rate and Low Fitness Suggest That Forest Water Bodies Comprise Ecological Traps for Pied Flycatchers. *Birds*, *3*(2), 221-233. https://doi.org/10.3390/birds3020014

Labocha, M. K., & Hayes, J. P. (2011). Morphometric indices of body condition in birds: a review. *Journal of Ornithology*, *153*(1), 1-22. https://doi.org/10.1007/s10336-011-0706-1

doi:10.6342/NTU202302673

Lagrue, C., & Presswell, B. (2016). Assessing parasite infections from avian faecal samples: The old methods are still the best. *Notornis*, *63*, 32-36.

Lessells, C. M., & Avery, M. I. (1989). Hatching Asynchrony in European Bee-Eaters Merops apiaster. *Journal of Animal Ecology*, *58*(3), 815-835. https://doi.org/10.2307/5126

Libman, M. D., Gyorkos, T. W., Kokoskin, E., & Maclean, J. D. (2008). Detection of pathogenic protozoa in the diagnostic laboratory: result reproducibility, specimen pooling, and competency assessment. *J Clin Microbiol*, *46*(7), 2200-2205. https://doi.org/10.1128/JCM.01666-07

Manzoli, D. E., Antoniazzi, L. R., Saravia, M. J., Silvestri, L., Rorhmann, D., & Beldomenico, P. M. (2013). Multi-level determinants of parasitic fly infection in forest passerines. *PLoS One*, *8*(7), e67104. https://doi.org/10.1371/journal.pone.0067104

Manzoli, D. E., Saravia-Pietropaolo, M. J., Arce, S. I., Percara, A., Antoniazzi, L. R., & Beldomenico, P. M. (2021). Specialist by preference, generalist by need: availability of quality hosts drives parasite choice in a natural multihost-parasite system. *Int J Parasitol*, *51*(7), 527-534. https://doi.org/10.1016/j.ijpara.2020.12.003

Marzal, A., Bensch, S., Reviriego, M., Balbontin, J., & De Lope, F. (2008). Effects of malaria double infection in birds: one plus one is not two. *J Evol Biol*, *21*(4), 979-987. https://doi.org/10.1111/j.1420-9101.2008.01545.x

McHardy, I. H., Wu, M., Shimizu-Cohen, R., Couturier, M. R., & Humphries, R. M. (2014). Detection of intestinal protozoa in the clinical laboratory. *J Clin Microbiol*, *52*(3), 712-720. https://doi.org/10.1128/jcm.02877-13

doi:10.6342/NTU202302673

Merino, S., Moreno, J., Sanz, J. J., & Arriero, E. (2000). Are avian blood parasites pathogenic in the wild? A medication experiment in blue tits (Parus caeruleus). *Proc Biol Sci*, *267*(1461), 2507-2510. https://doi.org/10.1098/rspb.2000.1312

Milenkaya, O., Catlin, D. H., Legge, S., & Walters, J. R. (2015). Body Condition Indices Predict Reproductive Success but Not Survival in a Sedentary, Tropical Bird. *PLoS One*, *10*(8), e0136582. https://doi.org/10.1371/journal.pone.0136582

Minias, P., Gach, K., Wlodarczyk, R., & Janiszewski, T. (2019). Colony size affects nestling immune function: a cross-fostering experiment in a colonial waterbird. *Oecologia*, *190*(2), 333-341. https://doi.org/10.1007/s00442-019-04402-3

Minias, P., Włodarczyk, R., & Janiszewski, T. (2015). Opposing selective pressures may act on the colony size in a waterbird species. *Evolutionary Ecology*, *29*(2), 283-297. https://doi.org/10.1007/s10682-014-9752-5

Møller, A. P., Merino, S., Brown, C. R., & Robertson, R. J. (2001). Immune defense and host sociality: a comparative study of swallows and martins. *Am Nat*, *158*(2), 136-145. https://doi.org/10.1086/321308

Nip, E. J., Frei, B., & Elliott, K. H. (2019). Seasonal and temporal variation in scaled mass index of Black-capped Chickadees (Poecile atricapillus). *The Canadian Field-Naturalist*, *132*(4), 368-377. https://doi.org/10.22621/cfn.v132i4.2015

Nuijten, R. J. M., Vriend, S. J. G., Wood, K. A., Haitjema, T., Rees, E. C., Jongejans, E., & Nolet, B. A. (2020). Apparent breeding success drives long-term population dynamics of a migratory swan. *Journal of Avian Biology*, *51*(11). https://doi.org/https://doi.org/10.1111/jav.02574

doi:10.6342/NTU202302673

O'Brien, V. A., & Brown, C. R. (2011). Group size and nest spacing affect Buggy Creek virus (Togaviridae: Alphavirus) infection in nestling house sparrows. *PLoS One*, *6*(9), e25521. https://doi.org/10.1371/journal.pone.0025521

Oniki-Willis, Y., Willis, E. O., Lopes, L. E., & Rózsa, L. (2023). Museum-Based Research on the Lice (Insecta: Phthiraptera) Infestations of Hummingbirds (Aves: Trochilidae)-Prevalence, Genus Richness and Parasite Associations. *Diversity*, *15*(1).

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos*, *118*(12), 1883-1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

Picman, J., Pribil, S., & Isabelle, A. (2002). Antipredation Value of Colonial Nesting in Yellow-Headed Blackbirds. *The Auk*, *119*(2), 461-472. https://doi.org/10.1093/auk/119.2.461

Pigeault, R., Cozzarolo, C. S., Choquet, R., Strehler, M., Jenkins, T., Delhaye, J., Bovet, L., Wassef, J., Glaizot, O., & Christe, P. (2018). Haemosporidian infection and co-infection affect host survival and reproduction in wild populations of great tits. *International journal for parasitology*, *48*(14), 1079-1087. https://doi.org/10.1016/j.ijpara.2018.06.007

Pigeault, R., Cozzarolo, C. S., Glaizot, O., & Christe, P. (2019). Effect of age, haemosporidian infection and body condition on pair composition and reproductive success in Great Tits Parus major. *Ibis*, *162*(3), 613-626. https://doi.org/10.1111/ibi.12774

doi:10.6342/NTU202302673

Postma, E., & van Noordwijk, A. J. (2005). Genetic Variation for Clutch Size in Natural Populations of Birds from a Reaction Norm Perspective. *Ecology*, *86*(9), 2344-2357. http://www.jstor.org/stable/3451023

Rassouli, M., Darvishi, M. M., & Lima, S. R. R. (2016). Ectoparasite (louse, mite and tick) infestations on female turkeys (Galliformes, Phasianidae. Meleagris gallopavo) in Iran. *Journal of parasitic diseases*, *40*(4), 1226-1229. https://doi.org/10.1007/s12639-015-0657-1

Reséndiz-Infante, C., & Gauthier, G. (2020). Temporal changes in reproductive success and optimal breeding decisions in a long-distance migratory bird. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-78565-y

Romagnano, A. (1999). Examination and Preventive Medicine Protocols in Psittacines. *Veterinary Clinics of North America: Exotic Animal Practice*, *2*(2), 333-355. https://doi.org/https://doi.org/10.1016/S1094-9194(17)30127-5

Rönkä, M., Saari, L., Hario, M., Hänninen, J., & Lehikoinen, E. (2011). Breeding success and breeding population trends of waterfowl: Implications for monitoring. *Wildlife Biology*, *17*, 225-239. https://doi.org/10.2981/09-064

Russell, R. E., DiRenzo, G. V., Szymanski, J. A., Alger, K. E., & Grant, E. H. C. (2020). Principles and Mechanisms of Wildlife Population Persistence in the Face of Disease [Policy and Practice Reviews]. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.569016

Sánchez, C. A., Becker, D. J., Teitelbaum, C. S., Barriga, P., Brown, L. M., Majewska, A. A., Hall, R. J., & Altizer, S. (2018). On the relationship between body condition and parasite infection in wildlife: a review and meta-analysis. *Ecology Letters*, *21*(12), 1869-1884. https://doi.org/10.1111/ele.13160

doi:10.6342/NTU202302673

Sarah, E. B., & Dale, H. C. (2023). Does Preening Behavior Reduce the Prevalence of Avian Feather Lice (Phthiraptera: Ischnocera)? *Journal of Parasitology*, *109*(3), 145-147. https://doi.org/10.1645/23-2

Schuster, R., & Krone, O. (2016). Infectious Diseases. In J. Samour (Ed.), *Avian Medicine (Third Edition)* (pp. 480). Mosby. https://doi.org/https://doi.org/10.1016/B978-0-7234-3832-8.00014-6

Smalley, I., Blake-Smalley, R., O'Hara-Dhand, K., Jary, Z., & Svircev, Z. (2013). Sand martins favour loess: How the properties of loess ground facilitate the nesting of sand martins/bank swallows/uferschwalben (Riparia riparia Linnaeus 1758). *Quaternary International*, *296*, 216-219. https://doi.org/https://doi.org/10.1016/j.quaint.2012.03.059

Sol, D., Jovani, R., & Torres, J. (2003). Parasite mediated mortality and host immune response explain age-related differences in blood parasitism in birds. *Oecologia*, *135*(4), 542-547. https://doi.org/10.1007/s00442-003-1223-6

Stope, M. B. (2023). The Connection between Immunocompetence and Reproduction in Wildlife. *Life*, *13*(3), 785. https://www.mdpi.com/2075-1729/13/3/785

Strong, A. M., & Sherry, T. W. (2000). Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology*, *69*(5), 883-895. https://doi.org/10.1046/j.1365-2656.2000.00447.x

doi:10.6342/NTU202302673

Suh, K. N., Kozarsky, P., & Keystone, J. S. (2015). Cyclospora cayetanensis, Cystoisospora (Isospora) belli, Sarcocystis Species, Balantidium coli, and Blastocystis Species. In J. E. Bennett, R. Dolin, & M. J. Blaser (Eds.), *Mandell, Douglas, and Bennett's Principles and Practice of Infectious Diseases (Eighth Edition)* (pp. 3184-3191.e3182). W.B. Saunders. https://doi.org/https://doi.org/10.1016/B978-1-4557-4801-3.00285-X

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13-21. https://doi.org/10.1007/s00265-010-1037-6

Tella, J. L. (2002). The evolutionary transition to coloniality promotes higher blood parasitism in birds. *Journal of Evolutionary Biology*, *15*(1), 32-41. https://doi.org/https://doi.org/10.1046/j.1420-9101.2002.00375.x

Tortosa, F. S., Pérez, L., & Hillström, L. (2003). Effect of food abundance on laying date and clutch size in the White Stork Ciconia ciconia. *Bird Study*, *50*(2), 112-115. https://doi.org/10.1080/00063650309461302

Townsend, A. K., Wheeler, S. S., Freund, D., Sehgal, R. N. M., & Boyce, W. M. (2018). Links between blood parasites, blood chemistry, and the survival of nestling American crows. *Ecol Evol*, *8*(17), 8779-8790. https://doi.org/10.1002/ece3.4287

Wang, Y.-P., Siefferman, L., Wang, Y.-J., Ding, T.-S., Chiou, C.-R., Shieh, B.-S., Hsu, F.-S., & Yuan, H.-W. (2009). Nest site restoration increases the breeding density of blue-tailed bee-eaters. *Biological Conservation*, *142*(8), 1748-1753. https://doi.org/10.1016/j.biocon.2009.03.013

doi:10.6342/NTU202302673

Ward, P., & Zahavi, A. (1973). THE IMPORTANCE OF CERTAIN ASSEMBLAGES OF BIRDS AS “INFORMATION-CENTRES” FOR FOOD-FINDING. *Ibis*, *115*(4), 517-534. https://doi.org/https://doi.org/10.1111/j.1474-919X.1973.tb01990.x

Williams, R. B. (2005). Avian malaria: clinical and chemical pathology of Plasmodium gallinaceum in the domesticated fowl Gallus gallus. *Avian Pathol*, *34*(1), 29-47. https://doi.org/10.1080/03079450400025430

Wolc, A., Jankowski, T., Arango, J., Settar, P., Fulton, J. E., O’Sullivan, N. P., & Dekkers, J. C. M. (2019). Investigating the genetic determination of clutch traits in laying hens. *Poultry Science*, *98*(1), 39-45. https://doi.org/https://doi.org/10.3382/ps/pey354

Wong, M. H. (2021). Tanks, propaganda and tourists: Welcome to Kinmen County. https://edition.cnn.com/travel/article/kinmen-travel-taiwan-china/index.html

World Health, O., Research, U. N. U. W. B. W. S. P. f., & Training in Tropical, D. (2015). Microscopy for the detection, identification and quantification of malaria parasites on stained thick and thin blood films in research settings (version 1.0): procedure: methods manual. World Health Organization. https://apps.who.int/iris/handle/10665/163782

Yabsley, M. J. (2008). Eimeria. In *Parasitic Diseases of Wild Birds* (pp. 162-180). https://doi.org/https://doi.org/10.1002/9780813804620.ch8

Yang, L., Zhou, L., & Song, Y. (2015). The effects of food abundance and disturbance on foraging flock patterns of the wintering Hooded Crane (Grus monacha). *Avian Research*, *6*(1), 15. https://doi.org/10.1186/s40657-015-0024-z

doi:10.6342/NTU202302673

Yuan, H. W., Brent Burt, D., Wang, L. P., Chang, W. L., Wang, M. K., Chiou, C. R., & Ding, T. S. (2006). Colony site choice of blue-tailed bee-eaters: influences of soil, vegetation, and water quality. *Journal of Natural History*, *40*(7-8), 485-493. https://doi.org/10.1080/00222930600681043

Yuan, H. W., Burt, D., Wang, L. P., Chang, W. L., Wang, M. K., Chiou, C. R., & Ding, T. S. (2006). Colony site choice of blue-tailed bee-eaters: Influences of soil, vegetation, and water quality. *Journal of Natural History - J NATUR HIST*, *40*. https://doi.org/10.1080/00222930600681043

Yuan, H. W., Wang, M. K., Chang, W. L., Wang, L. P., Chen, Y. M., & Chiou, C. R. (2006). Soil composition affects the nesting behavior of blue-tailed bee-eaters (Merops philippinus) on Kinmen Island. *Ecological Research*, *21*(4), 510-512. https://doi.org/10.1007/s11284-006-0183-9

Zylberberg, M., Derryberry, E. P., Breuner, C. W., Macdougall-Shackleton, E. A., Cornelius, J. M., & Hahn, T. P. (2015). Haemoproteus infected birds have increased lifetime reproductive success. *Parasitology*, *142*(8), 1033-1043. https://doi.org/10.1017/S0031182015000256

林昀萱. (2022). 金門栗喉蜂虎生殖群規模對生殖成功之影響 國立臺灣大學]. http://dx.doi.org/10.6342/NTU202202555

蔡佩妤. (2007). 金門島栗喉蜂虎生殖經驗對於繁殖棲地忠實性之影響 (Publication Number 2007 年) 國立臺灣大學]. AiritiLibrary.

袁孝維, 王力平, & 丁宗蘇. (2003). 金門島栗喉蜂虎（Merops philipennus）繁殖生物學研究. 國家公園學報, *13(2)*, 71-84.

doi:10.6342/NTU202302673

Figures

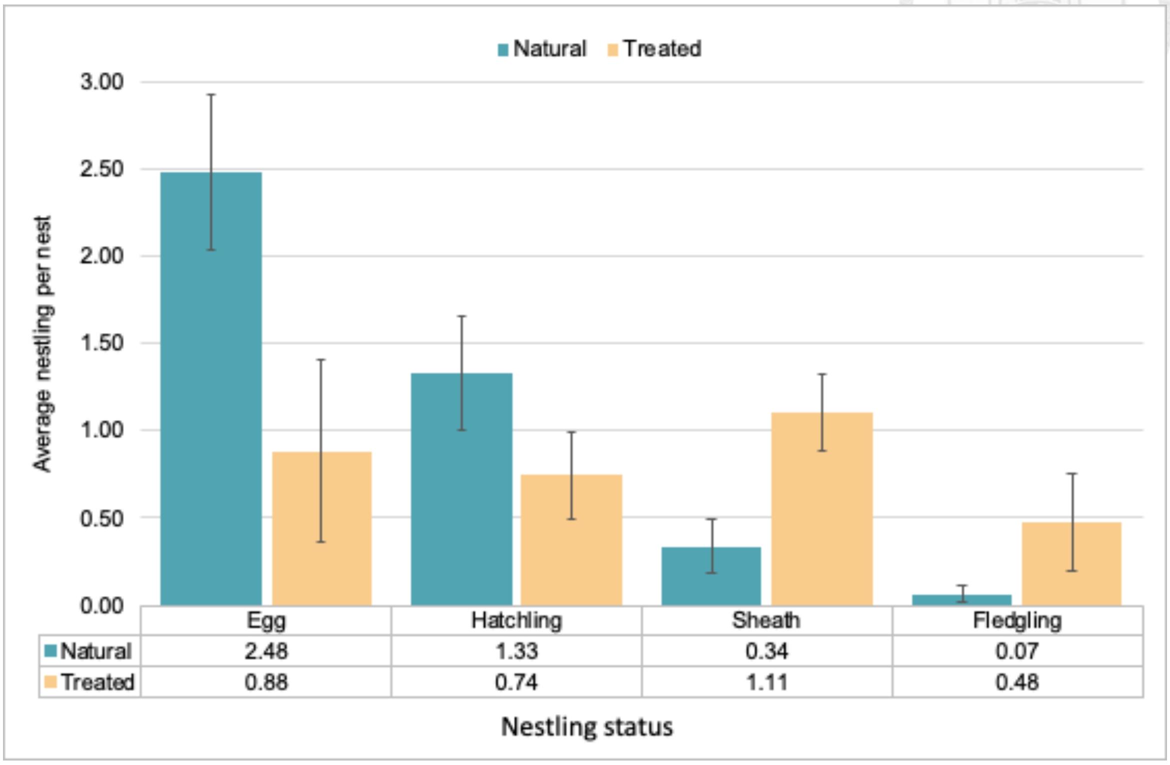


Figure 1. Histogram showing the average eggs, hatchlings, sheaths and fledglings per nest observed in natural (green bars) and treated (yellow bars) colonies on Kinmen island. The capped lines represent the standard error of each chick status. Nestling status in natural colonies was collected between June 22nd - 27th and treated colonies between July 2nd - 5th, 2022.

doi:10.6342/NTU202302673

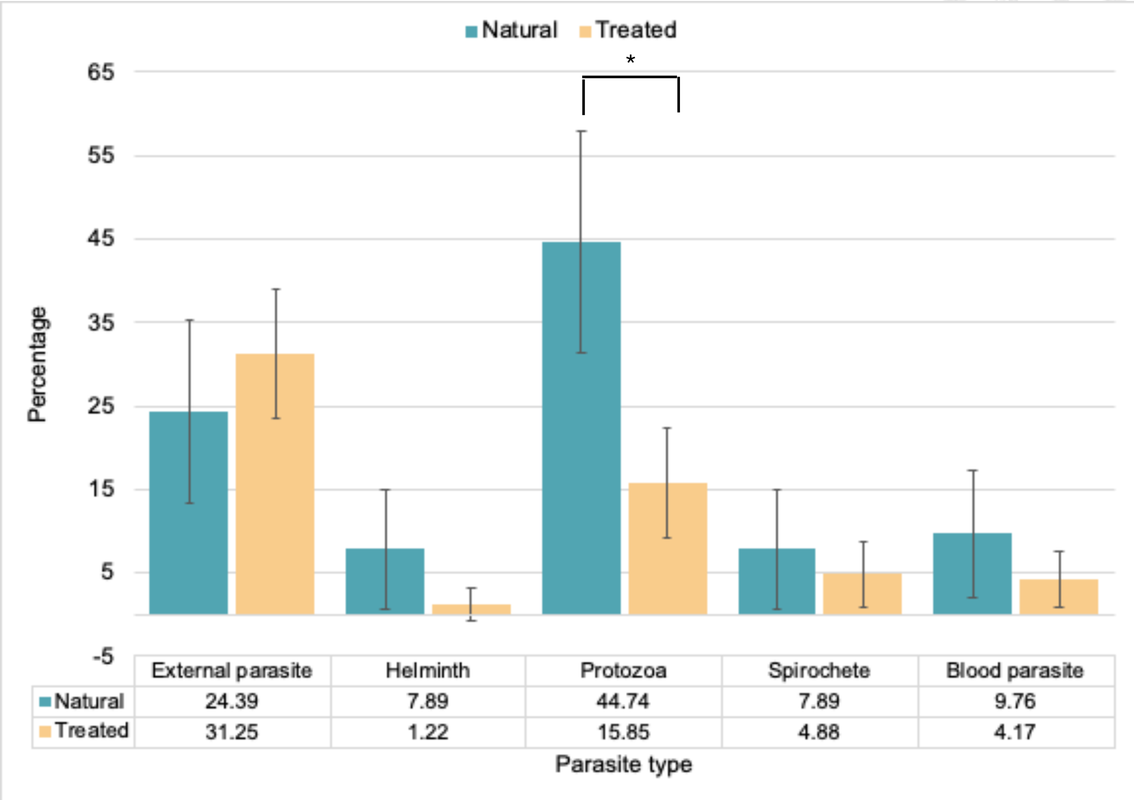


Figure 2. Prevalence of each parasite detected in blue-tailed bee-eaters residing in natural and treated colonies where the asterisk (*) indicated the statistically difference (p = 0.0015). The green bars represent each parasite prevalence observed in natural colonies and yellow bars represent treated colonies. Vertical arrow bars represent the 90% confidence interval.

doi:10.6342/NTU202302673

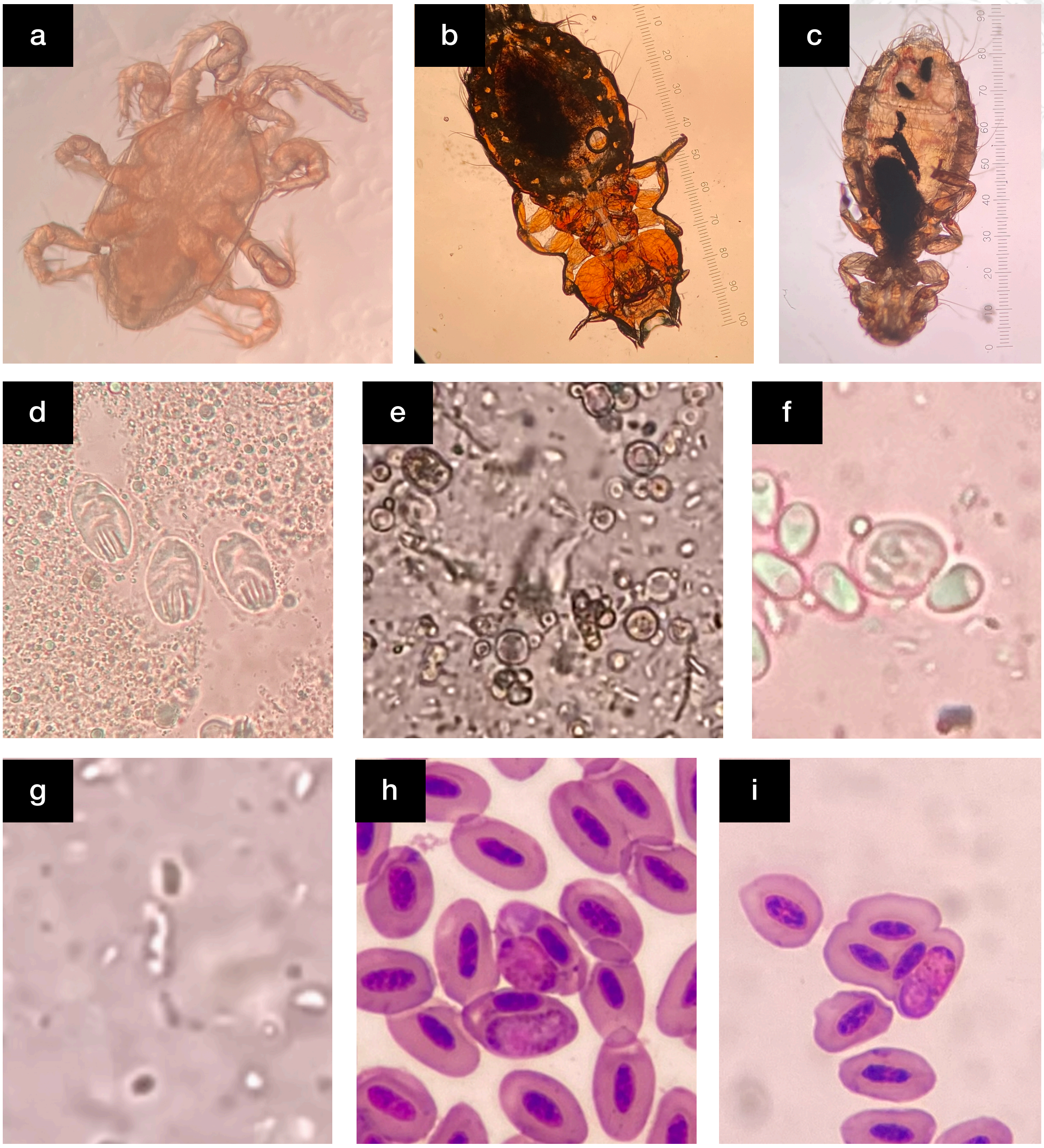


Figure 3. Microscopic photos of parasites detected in blue-tailed bee-eater nest soil, fecal sample, and blood sample. (a, b) Suspected Dermanyssus mite and Amblecera feather lice detected in nest soil (100X). (c) Amblecera found commonly in birds feather. (d) Hexacanth larva of tapeworm found in feces (400X). (e) Unidentified flagellated protozoa in feces (400X). (f) Unidentified protozoa cyst (400X). (g) Motile spirochete bacteria in fecal sample (400X). (h, i) Intracellular Haemosporidian blood parasite suspected to be Plamodium spp gametocytes invaded the red blood cells where the nucleus were displaced.

doi:10.6342/NTU202302673

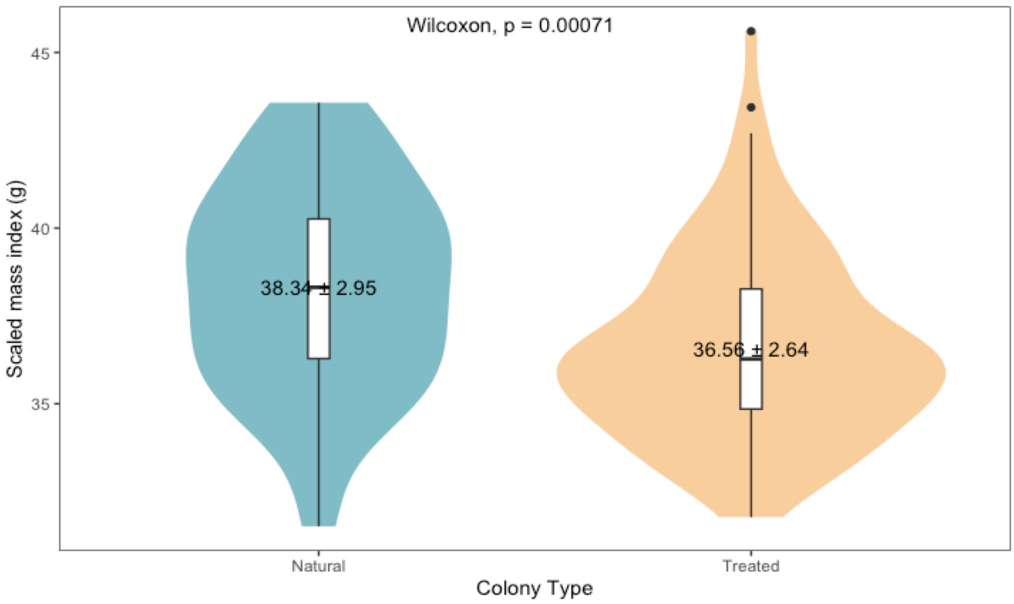


Figure 4. Comparison of SMI (g) observed in blue-tailed bee-eaters residing between natural (n = 40) and treated breeding colonies (n = 96). The bold horizontal lines inside the boxes represent medians SMI of each colony type. The top and bottom sides of the boxes show the 75th and 25th percentiles, respectively. The box as a whole shows where the middle 50% of the data lies. Vertical lines indicate maximum and minimum SMI values. The colored area indicated the density distribution of each colony type.

doi:10.6342/NTU202302673

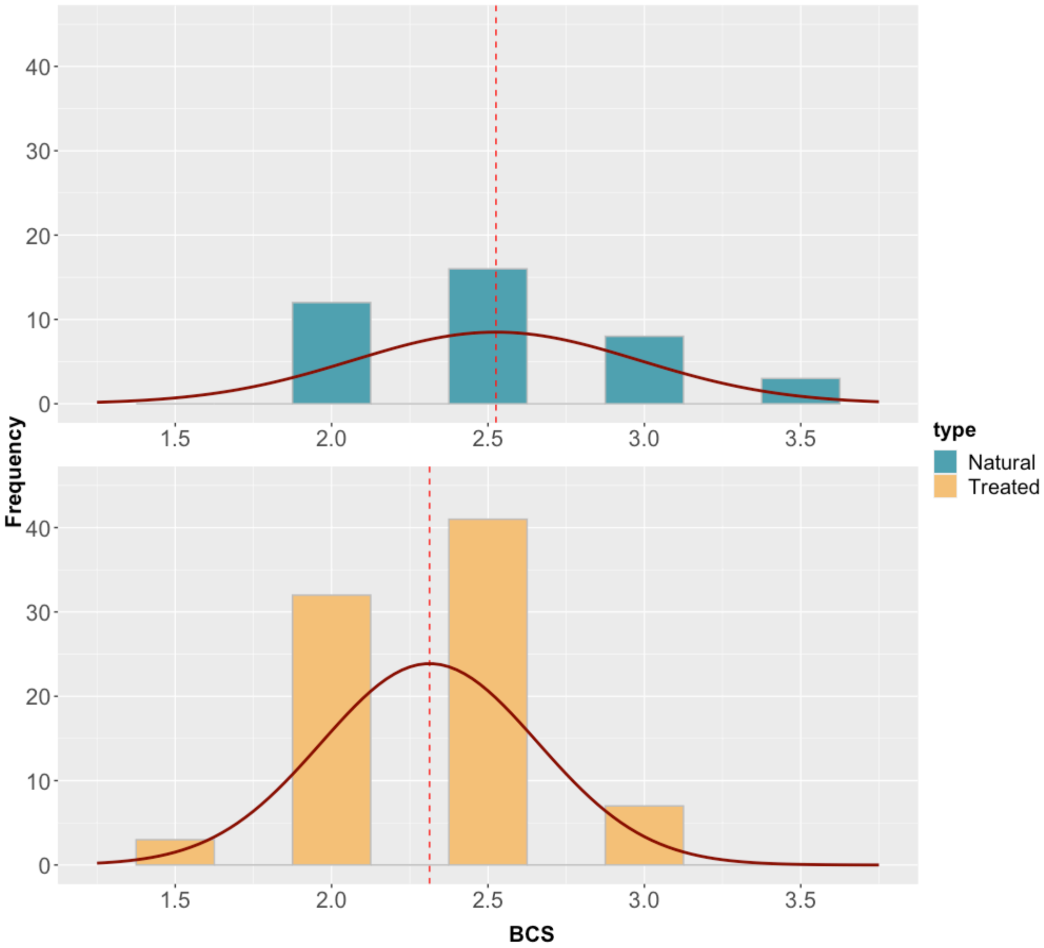


Figure 5. Number of bird (frequency) and distribution observed in each body condition score (BCS) from natural breeding colonies (n = 39) and treated colonies (n = 83). The red dashed line indicated the mean±SD (2.53 ±0.46 and 2.31 ±0.35 respectively) and the dark red line indicated density distribution.

doi:10.6342/NTU202302673

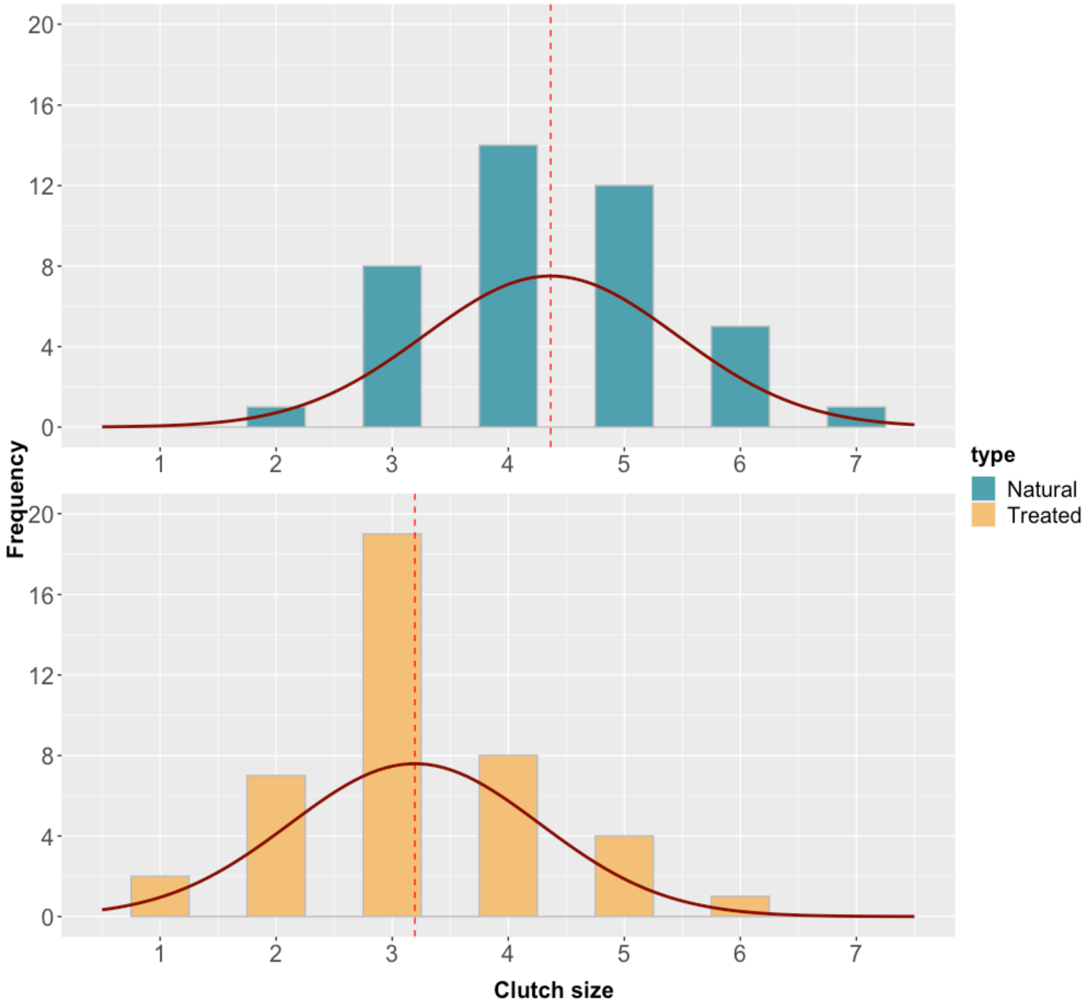


Figure 6. Number of bird (frequency) observed in each brood size from natural breeding colonies (n = 41) and treated colonies (n = 41). The red dashed line indicated the mean±SD (4.37 ±1.09 and 3.20 ±1.08 respectively) and the dark red line indicated density distribution.

doi:10.6342/NTU202302673

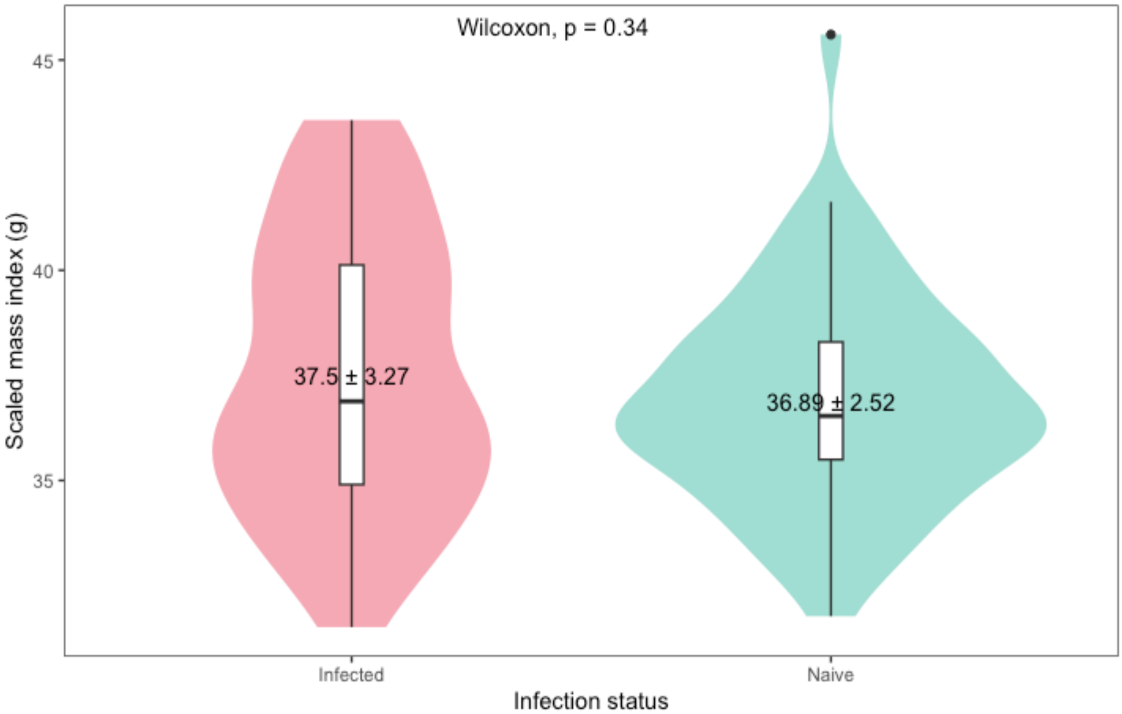


Figure 7. Comparison of SMI (g) observed in blue-tailed bee-eaters residing between natural (n = 40) and treated breeding colonies (n = 96). The bold horizontal lines inside the boxes represent medians SMI of each colony type. The top and bottom sides of the boxes show the 75th and 25th percentiles, respectively. The box as a whole shows where the middle 50% of the data lies. Vertical lines indicate maximum and minimum SMI values. The colored area indicated the density distribution of each colony type.

doi:10.6342/NTU202302673

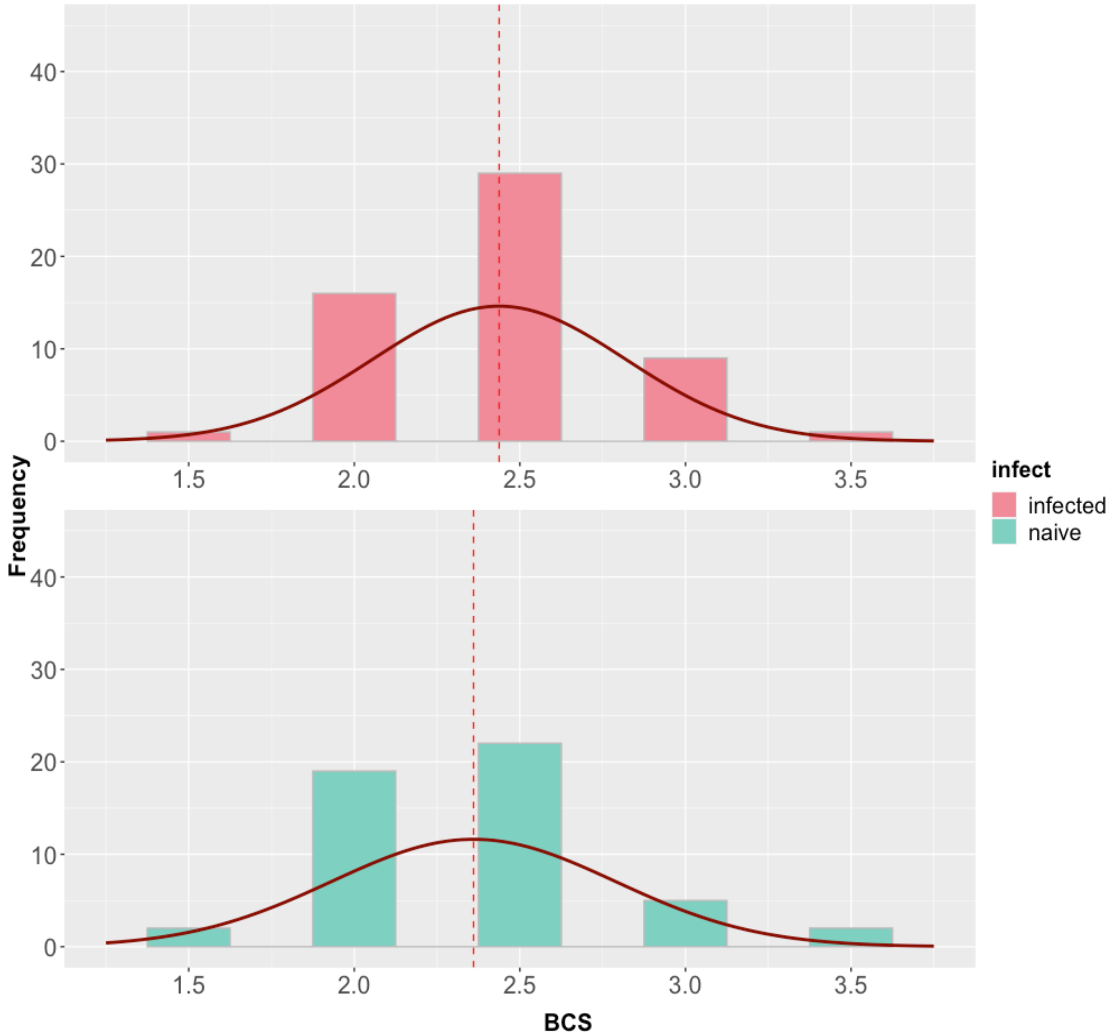


Figure 8. Number of bird (frequency) observed in each body condition score (BCS) of infected birds (n = 56) and naive birds (n = 50). The dashed red line indicated the mean±SD (2.44 ± 0.38 and 2.36 ± 0.43 respectively) and dark red solid line indicated density distribution.

doi:10.6342/NTU202302673

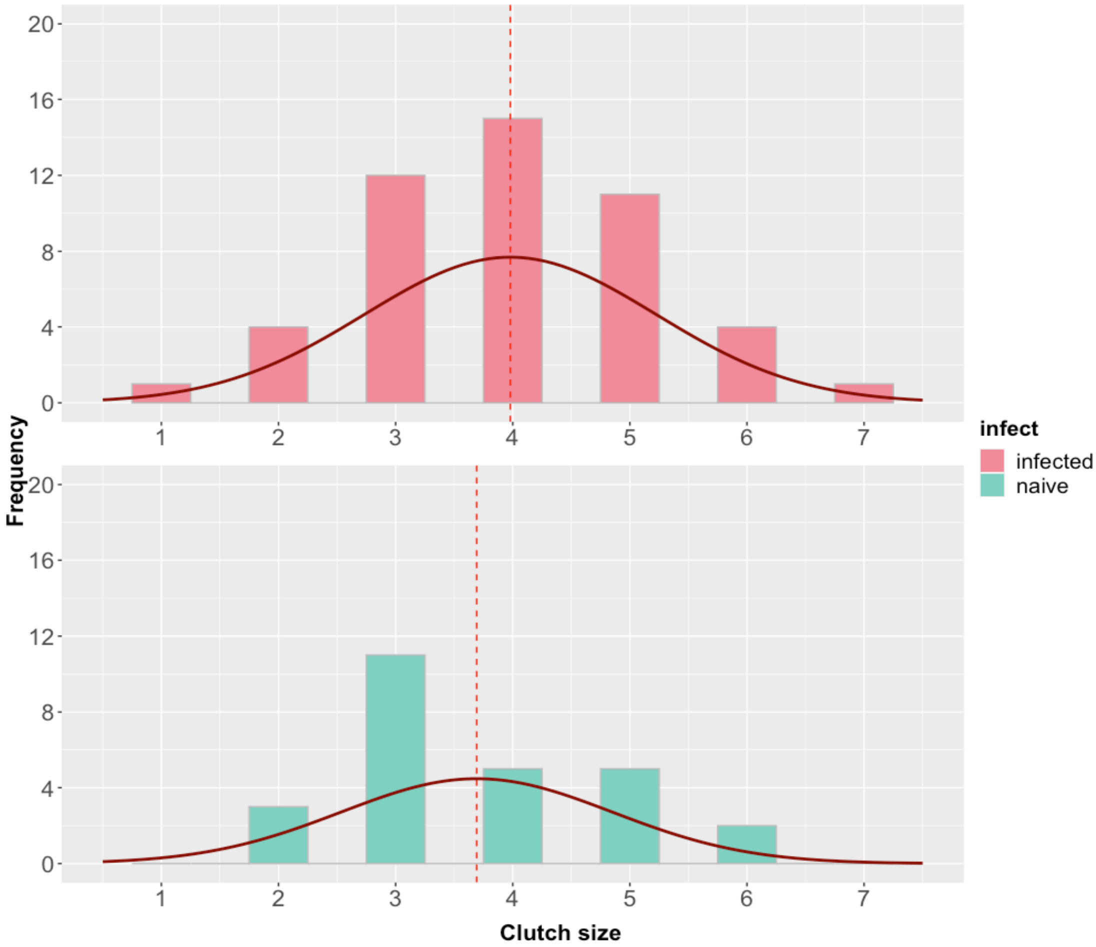


Figure 9. Number of bird (frequency) observed in each brood size of infected birds (n = 48) and naive birds (n = 26). The red dashed line indicated the mean±SD (3.98 ± 1.25 and 3.69 ± 1.16 respectively) and dark red line indicated density distribution.

doi:10.6342/NTU202302673

Figure 10. Aerial landscape captured from Google map showing the location of two breeding colonies (red dots) where foraging area including water sources are possibly overlapping (Fengshang; FS, Qingqing farm; CC). The yellow arrows indicated the reservoirs and agriculture ponds where birds residing in two colonies might share.

doi:10.6342/NTU202302673

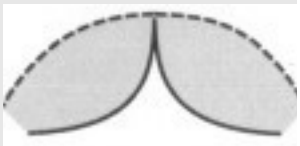
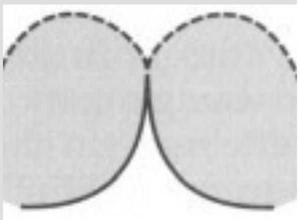
Tables

Table 1. The total lists of breeding colonies of blue-tailed bee-eaters in Kinmen island, total nest count, and number of samples.

Breeding site	Type of nest	Est. nest density (nests/m^2)	Total nest count	Number o samples
Tianpu north (TPN)	Natural	0.028	17	11
Tianpu south (TPS)	Natural	0.029	23	13
Fengshang (FS)	Natural	0.004	17	10
Oucuo beach north (OCN)	Natural	0.005	97	7
Youth farm (YFL)	Treated	1.19	476	69
Qingqing farm (CC)	Treated	0.4	12	8
Triangle castle (TC)	Treated	1.78	151	19
Total			793	137

doi:10.6342/NTU202302673

Table 2. The pectoral muscle score criteria using the keel ridge and pectoral muscle characteristics. The rightmost column indicates the skyline views of breast bone and muscle for reference (Romagnano, 1999).

Score	Interpretation	Characteristics	Top view
1	Emaciated	Very sharp and prominent breast bone when touch. Pectoral muscle concave and no fat cover.	
2	Thin	Breast bone is easily to locate and sharp. Pectoral muscle concave with no or little fat cover.	
3	Ideal	Breast bone is easily felt but not sharp. Round pectoral muscle	
4	Overweight	Pressure is needed to feel the breast bone. Well rounded, a bit convex pectoral muscle with some fat cover.	
5	Obese	Very hard or not possible to locate the breast bone. Very rounded, flush pectoral muscle with possibility to see fat under the skin.	

doi:10.6342/NTU202302673

Table 3. Parasite prevalence shown in percentage detected in blue-tailed bee-eater droppings and blood collected in June - July 2022 with 90% confidence interval (CI). N indicated number of samples positive and the total samples examined were in the parentheses. P-value (*p*) is calculated to see whether there was a significant difference between two colony types. Except for external parasite, all pathogen examined from natural colonies had higher prevalence than treated colonies. Only protozoa infection showed a significant difference between colony types.

Parasite	Colony type	N	Prevalence	CI	Pathogens	*p*
External parasite	Natural	10 (41)	24.39%	13.35 - 35.42	Amblycera, Hippobosca	0.1382†
	Treated	30 (96)	31.25%	23.47 - 39.03		
Helminth	Natural	3 (38)	7.89%	0.70 - 15.08	Cestoda	0.0932††
	Treated	1 (82)	1.22%	-0.77 - 3.21*		
Protozoa	Natural	17 (38)	44.74%	31.47 - 58.01	*Giardia spp.* and unidentified cyst	0.0015†
	Treated	13 (82)	15.85%	9.22 - 22.48		
Spirochete	Natural	3 (38)	7.89%	0.70 - 15.08	*Spirochete spp.*	0.0932††
	Treated	4 (82)	4.88%	0.97 - 8.79		
Blood parasite	Natural	4 (38)	9.76%	2.14 - 17.38	*Plasmodium spp.*	0.2396††
	Treated	4 (96)	4.17%	0.81 - 7.53		

*Negative confidence limit seen from helminth prevalence in treated colony was suspected to be caused by the low number of positive birds.
† Pearson's Chi Square test, †† Fisher's Exact test

doi:10.6342/NTU202302673

Table 4. Comparisons of means (±SD, with number of birds observed in parentheses) of scale mass index (SMI), body condition score (BCS), and brood size between blue-tailed bee-eaters from natural and treated breeding colonies, and between infected and naive population using Mann-Whitney U test. The asterisk (*) indicated the significant different between two groups of $p<0.05$ as a cut-off. Hedges' g effect size was calculated to see the magnitude of difference.

Variable	Types of breeding colonies				Infection status			
	Natural	Treated	*p*	Effect size	Infected	Naive	*p*	Effect size
SMI	38.34 ± 2.95 (40)	36.56 ± 2.64 (96)	<0.001*	0.65	37.50 ± 3.27 (61)	36.89 ± 2.52 (58)	0.3400	0.20
BCS	2.53 ± 0.46 (39)	2.31 ± 0.35 (83)	0.0229*	0.56	2.44 ± 0.38 (56)	2.36 ± 0.43 (50)	0.2406	0.19
Brood size	4.37 ± 1.09 (41)	3.20 ± 1.08 (41)	<0.0001*	1.08	3.98 ± 1.25 (48)	3.69 ± 1.16 (26)	0.2746	0.24

doi:10.6342/NTU202302673

Table 5. The prevalence of each organism in adult blue-tailed bee-eaters regarding each breeding site. The numbers are shown in percentages.

Breeding site	External parasite	Helminth	Protozoa	Spirochete	Blood parasite
Natural					
FS	30.00	0.00	60.00	20.00	10.00
OCN	42.86	0.00	50.00	0.00	28.57
TPN	0.00	33.33	22.22	0.00	9.09
TPS	30.77	0.00	46.15	7.69	0.00
Treated					
CC	25.00	0.00	75.00	0.00	12.50
TC	21.05	0.00	11.11	0.00	0.00
YFL	34.78	1.79	8.93	7.14	4.35

doi:10.6342/NTU202302673

Table 6. Generalized linear mixed model estimates for the influence of external parasite, helminth, protozoa, spirochete and blood parasite infection explaining variation of physical fitness and reproductive performance in the blue-tailed bee-eater. Each first-level model contains single parasite predictor influencing SMI and BCS. These models are ranked according to the lowest to the highest AICc value.

Model	Estimate Std.	SE	AIC	ΔAIC	W	σ^2	p
mSMI: Scale mass index[a]							
External parasite	0.7024	0.5527	585.11	0.00	0.30	1.287	0.204
Blood parasite	0.1523	0.1259	585.26	0.15	0.28	1.301	0.226
Protozoa	-0.1394	0.2650	586.43	1.33	0.15	1.410	0.599
Spirochete	0.1062	0.4354	586.65	1.54	0.14	1.241	0.807
Helminth	0.1156	1.4648	586.70	1.60	0.13	1.280	0.937
mBCS: Body condition score[b]							
External parasite	0.0699	0.0136	118.52	0.00	0.22	<0.0001	0.750
Protozoa	0.0116	0.0575	118.74	0.22	0.20	<0.0001	0.968
Helminth	0.0421	0.0325	118.77	0.25	0.19	<0.0001	0.926
Spirochete	0.0130	0.0102	118.77	0.25	0.19	<0.0001	0.930
Blood parasite	-0.0022	0.0289	118.78	0.26	0.19	<0.0001	0.841

The number of observation in each model (a, b, c) were 119, 120, and 120 respectively. The variance (σ^2) of random effects was given on each model. Each model used different family objects as follow: a) Gaussian; b) Gamma; c) Negative binomial.

doi:10.6342/NTU202302673

Table 6 (cont). Generalized linear mixed model estimates for the influence of external parasite, helminth, protozoa, spirochete and blood parasite infection explaining variation of physical fitness and reproductive performance in the blue-tailed bee-eater. Each first-level model contains single parasite predictor influencing brood size. These models are ranked according to the lowest to the highest AICc value.

Model	Estimate Std.	SE	AIC	ΔAIC	W	σ^2	p
mBR: Brood size[c]							
Spirochete	-0.0461	0.0908	269.08	0.00	0.27	<0.0001	0.629
Protozoa	0.0154	0.0461	269.25	0.17	0.25	<0.0001	0.739
External parasite	-0.0343	0.1370	269.29	0.21	0.24	<0.0001	0.791
Blood parasite	0.0033	0.0224	269.35	0.27	0.24	0.0001	0.890

The number of observation in each model (a, b, c) were 119, 120, and 120 respectively. The variance (σ^2) of random effects was given on each model. Each model used different family objects as follow: a) Gaussian; b) Gamma; c) Negative binomial. GLMM of helminth infection influenced on brood size was removed from the model comparison due to the model convergence problem.

doi:10.6342/NTU202302673

Table 7. Body condition score and body mass (g) of recaptured birds with time intervals separated by the breeding site. All individuals were not paired and resided in separate burrows. BCS evaluated from two individuals were consistent (C27012 and C42448) while their body mass still decreased.

Ring code	Initial BCS	Recapture BCS	Initial weight (g)	Recapture weight (g)	Interval (days)
<u>TC</u>					
C27059	2.7	2.0	36.8	35.6	4
<u>TPN</u>					
C27002	3.5	2.0	36.0	34.5	7
C27010	3.5	2.0	37.2	35.5	7
<u>TPS</u>					
C27011	2.5	2.0	35.0	33.1	6
C27012	2.5	2.5	39.8	36.5	6
C27013	3.0	2.5	41.5	38.5	6
C27014	3.0	2.0	44.1	38.6	6
C42448	2.5	2.5	39.2	38.3	6

doi:10.6342/NTU202302673