

TIME-LAPSE IMAGERY OF PERUVIAN BOOBIES *SULA VARIEGATA* REVEALS NEST ABANDONMENT CAUSED BY TICK HYPERINFESTATION

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ABSTRACT

BURGA-DOMÍNGUEZ, C., GONZALES-DELCARPIO, D.D. & ZAVALAGA, C.B. 2020. Time-lapse imagery of Peruvian Boobies *Sula variegata* reveals nest abandonment caused by tick hyperinfestation. *Marine Ornithology* 48: 303–311.

Severe tick infestation in seabird colonies causes discomfort in reproductive adults, offspring mortality, and nest abandonment. This study used time-lapse cameras to examine the relationship between *Ornithodoros amblus* tick infestation and Peruvian Booby *Sula variegata* nest abandonment in four locations along the Peruvian coast between August 2016 and November 2018. The percent occurrence of discomfort in nesting birds (preening and standing on the nest) recorded by the cameras was used as an indicator of tick infestation. The tick density inside and outside the abandoned colonies was also evaluated. In five of the six colonies, complete nest abandonment occurred over an interval of two to three weeks. The percent occurrence of discomfort behavior was exponentially related to the percentage of nest abandonment, indicating that reproductive failure was related to tick hyperinfestation. This conclusion was reinforced by the fact that in a colony where no discomfort behaviors were recorded, there was no nest abandonment (53% of successful nests, $n = 17$). The tick density was higher inside (mean $\pm$ SD: 105.41 ± 92.8 ticks/500 mL of guano) than outside (43.08 ± 39.8 ticks/500 mL of guano) of the recently abandoned colonies, confirming that nest desertion was caused by tick hyperinfestation. The results of this study reveal that the use of time-lapse cameras in booby colonies is feasible not only for the determination of reproductive success but also for the identification of causes of nest abandonment.

Key words: Peruvian Booby, ectoparasites, tick, time-lapse camera, *Sula variegata*, *Ornithodoros amblus*, nest desertion

INTRODUCTION

Guano birds, which are among the most numerous groups of seabirds on the Peruvian coast, are represented by the Guanay Cormorant *Leucocarbo bougainvillii*, Peruvian Booby *Sula variegata*, and Peruvian Pelican *Pelecanus thagus* (Duffy *et al.* 1984, Crawford & Jahncke 1999). These birds, endemic to the Humboldt Current system, are mainly distributed from Lobos de Tierra Island, Peru ($06^{\circ}8'S$) to Mocha Island ($38^{\circ}30'S$), Chile (Murphy 1936, Jahncke 1998). In Peru, they nest on islands and walled-off headlands in highly dense colonies ranging upward to hundreds of thousands of birds (Passuni *et al.* 2018). In the 1950s, the abundance of these birds was estimated to be more than 30 million (Duffy 1987, Tovar & Cabrera 2005). However, recent estimates put the population at ≤ 5 million birds (Passuni *et al.* 2016). This dramatic decrease has been attributed to competition with the industrial fishing of Peruvian anchovy *Engraulis ringens* (Duffy 1983a, Goya 2000, Bertrand *et al.* 2012, Barbraud *et al.* 2018), which predominates in the diet of these birds (García-Godos & Goya 2000). Additionally, exacerbated by fishery depletion of prey, large-magnitude El Niño events have caused nest desertion and, in the worst case, death or dispersion of adults due to lack of food (Tovar & Cabrera 1985, Apaza & Figari 1999). Other factors are also known to exert adverse effects on guano birds, such as incidental entanglement (Jordán & Fuentes 1966, Majluf *et al.* 2002, Goya *et al.* 2016), poaching of adults and collection of eggs (Duffy *et al.* 1984, Cushman 2005), disturbance of colonies (Crawford *et al.* 1983), introduction of invasive species (Stucchi & Figueroa 2006), and infestation by ectoparasites (Duffy 1983b).

Infestation by ectoparasites causes nest desertion in several species of seabirds, thus controlling their populations via nesting area

restriction, colony desertion, and juvenile death (Feare 1976, King *et al.* 1977, Duffy & Campos De Duffy 1986, Ramos & Drummond 2017). In addition, ectoparasites cause the death of fledglings and adults due to anemia (Wanless *et al.* 1997) or as vectors that transmit organisms able to cause infection (Moss *et al.* 1986). For example, hyperinfestation of the tick *Ixodes uriae* (3500 tick larvae found in a recently deceased individual) was the cause of death in adult King Penguins *Aptenodytes patagonicus* (Gauthier-Clerc *et al.* 1998). In the Brown Pelican *Pelecanus occidentalis*, a negative effect on chick growth rate was observed during early development and on hatching success from *Carios capensis*, a tick infesting nests treated with and without insecticide (Eggert & Jodice 2008). Ticks (Class Arachnida, Order Ixodida) affect at least 146 species of seabirds around the world and are responsible for the spread of pathogens (Clifford *et al.* 1980, Dietrich *et al.* 2011, Dietrich *et al.* 2014, Nava *et al.* 2017). The high nest densities, extensive nesting periods, and colony fidelity of these birds offer ticks optimal conditions for development (Duffy 1983b, Dietrich *et al.* 2011). Additionally, tick characteristics, such as a fast multiplication rate and large numbers, allow them to proliferate almost without limit (Khalil & Hoogstraal 1981, Nava *et al.* 2017).

The presence of other ectoparasites has been reported on the islands and headlands of the Peruvian coast, such as lice *Tetrophthalmus titan* in Guanay Cormorant, Peruvian Booby, Blue-footed Booby *Sula nebouxii*, and Peruvian Pelican colonies (Murphy 1925, Stucchi & Figueroa 2006). However, studies have focused on the distribution of these ectoparasites but not on their interaction with birds. Increased preening behavior related to tick infestation was recorded in Brown Pelicans in Mexico (King *et al.* 1977), with these marked behavioral changes not only facilitating researcher observation but also unequivocally demonstrating the tick effects.

In Peru, ticks of the genus *Ornithodoros* cause guano bird nesting losses and chick mortality (Duffy 1983b, Iannaconne & Dale 1997). In colonies with high tick infestation, birds tend to be more restless, temporarily move away from nests, and expose nests to aerial predators (Duffy 1983b). Previous studies showed that the time invested in preening by parents increases notably in the three species of guano birds before nest desertion due to ticks (Duffy

1983b). The response level of birds to tick infestation depends on the life cycle stage of these ectoparasites. Larvae preferentially parasitize chicks, whereas nymphs and adults parasitize adults, with tick larvae and adults feeding on host blood for 3–6 d and 15–55 min, respectively (Clifford *et al.* 1980, Khalil & Hoogstraal 1981). After feeding, the adult ticks and larvae stay sheltered under the guano.

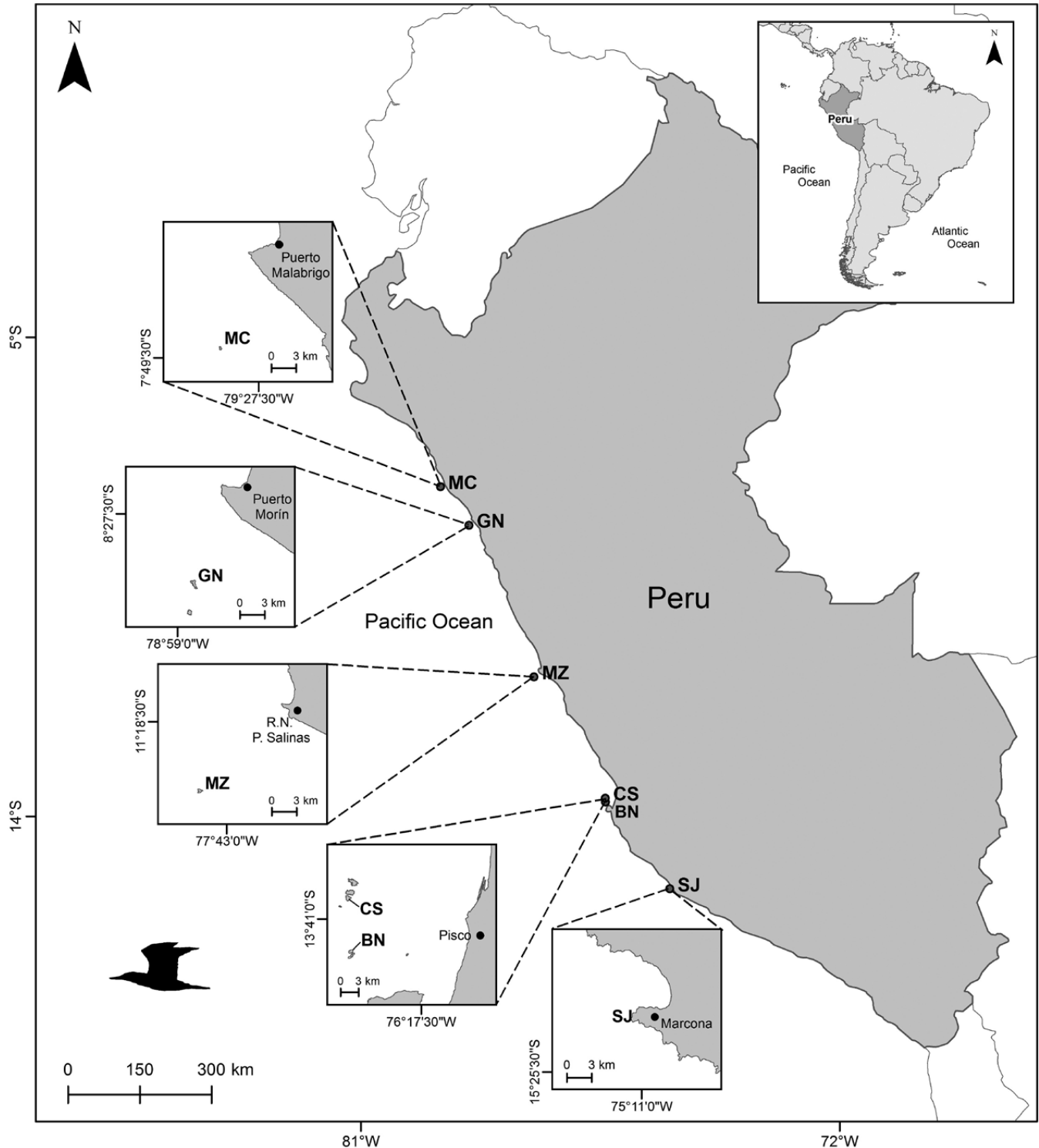


Fig. 1. Study site locations: MC = Macabí Island, GN = Guañape Norte Island, MZ = Mazorca Island, CS = Chincha Sur Island, BN = Ballestas Norte Island, and SJ = Punta San Juan. In MC, GN, MZ, and SJ, data were obtained from time-lapse cameras; guano samples were collected at CS, BN, GN, and MZ.

The relationship between nest abandonment and tick infestation has traditionally been quantified by direct observation, by counting the number of ticks either on the substrate or in nests, as in the case of guano birds (Iannacone & Ayala 2004) and in puffins and gulls (Order Charadriiformes) (Muzaffar & Jones 2007). Additionally, the number of ticks is also directly counted in offspring, as in the case of the Blue-footed Booby (Duffy & Campos De Duffy 1986, Ramos & Drummond 2017) and adult King Penguins (Gauthier-Clerc *et al.* 1998). These methods provide reliable indices of tick infestation intensity, but they are invasive because it is necessary to enter the colonies, inevitably disturbing the birds.

Time-lapse cameras are low-cost tools that are easy to operate and have good resolution for the study of animal behavior (Reif & Tornberg 2006). These cameras automatically record photographs at fixed time intervals, thereby documenting behavioral patterns and allowing the calculation of reproductive success in some seabird species (Huffeldt & Merkel 2013). Merkel *et al.* (2016) used time-lapse cameras to estimate the reproductive success of cliff-nesting seabirds in remote areas for three years and argued that the method can be used for other colonial birds having open nests. Perkins *et al.* (2005) used this technology to determine the causes underlying the loss of Horned Grebe *Podiceps auritus* nests and found that for this species, the most important variables were predation and changes in water level. Black *et al.* (2017) used a network of time-lapse cameras to monitor the displacement and phenology of the Gentoo Penguin *Pygoscelis papua* in Argentine Patagonia during the non-breeding and breeding periods, and evaluated the environmental and temporal factors involved in the reproduction of this species. The camera network revealed patterns of attendance during the non-breeding season, data that was difficult to obtain during the winter (Black *et al.* 2017). In Peru, time-lapse cameras have been used to successfully evaluate the duration of feeding trips of Peruvian Boobies (Ardiles 2019).

In the present study, images from time-lapse cameras set at four locations in the Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras (RNSIIPG) were acquired between 2016 and 2018. Images were used to document the behavior of birds before and during the nest desertion period and to examine the relationship between Peruvian Booby nest abandonment and tick infestation. Additionally, guano samples were collected in two additional locations in 2017, inside and outside the recently abandoned colonies, to obtain a tick density index for comparison with studies conducted in previous years. We postulated that during the nest abandonment period, there would be a drastic change in the behavior (greater preening frequency) of booby pairs and that this drastic change in behavior would be absent in colonies where nest abandonment did not occur.

METHODS

Study site and study period

The study was conducted between August 2016 and November 2018 on five guano islands and one guano headland within RNSIIPG: Macabi Island (07°48'47"S, 079°29'57"W), Guanape Norte Island (08°32'41"S, 078°57'49"W), Mazorca Island (11°23'01"S, 077°44'41"W), Punta San Juan (15°22'00"S, 075°11'28"W), Ballestas Norte Island (13°44'00.96"S, 076°23'49.2"W), and Chíncha Sur Island (13°39'02.88"S, 076°24'04.32"W). The selection of these locations included a sample of representative colonies of Peruvian Boobies in the north, center, and south Peruvian coast (Fig. 1).

Set-up of time-lapse cameras

Time-lapse cameras (Brinno, MAC200DN® <https://www.brinno.com/>) with a photo resolution of 1.3 megapixels, focal length of 28 mm, f2.0 aperture, focus distance of 60 cm, and field of view (FOV) of 75° were used to monitor nests. The time interval for photograph acquisition was 15 min during daylight hours (local time: 05h30 to 19h00, GMT -05h00). Each photograph contained a digital printout of the date and time. All photographs acquired in one day were compiled automatically by the camera into a video with a resolution of 720p (1280 × 720 pixels). The cameras operated with two D batteries.

The photographs were stored on a Sony® SD HC1 memory card with a storage capacity of 32 GB. Although these cameras are waterproof and can withstand adverse weather, they were placed inside plastic-covered wooden boxes to protect the camera lens from wind, guano, and moisture. The boxes were anchored on wooden posts or tied to the concrete structures of island guard houses (balconies, windows, posts) in strategic locations under the following considerations: i) placement near the guard houses to allow easy access to the camera without disturbing the boobies or other seabird species; ii) placement near colonies on the roofs of houses, water tanks, or cliffs; iii) placement to ensure good colony visibility (i.e., the camera was typically placed at a height 3–8 m above the colony and 3–15 m from the colony edge); and iv) cameras were set up during courtship or early incubation stages. At these distances, the cameras were able to capture 20 to 70 nests within a photographic frame. The battery life of the camera with the frequency of photo acquisition used was approximately eight months; therefore, the islands were visited at shorter intervals to replace the batteries and to download the photos from the memory card.

The number and location of the cameras used at the study sites were as follows: one camera on Gualaípe Norte Island was placed on the edge of a balcony 12 m above a reproductive group of approximately 120–150 nests (10%–15% of the population of boobies on the island during the study period); one camera on Macabí Island was placed on the edge of a balcony 3 m above a group of 80–90 nests (5%–10% of the total reproductive population during the study period); two cameras were placed on Mazorca Island, one on the window frame of a guard house aimed at a group of 90–100 nests located on the roof of a kitchen (less than 1% of the reproductive population during the period of study) and another on a stone wall pointing towards the roof of a water tank where a group of 70–80 nest was located; and one camera on Punta San Juan faced a cliff where 20–22 booby nests were located. Thus, five reproductive groups of boobies were monitored in four locations. On Gualaípe Norte Island, two reproductive seasons (2016 and 2018) were monitored in the same area. Because ticks showed a clumped distribution over the islands, two reproductive groups within the same locality, or the same group in two different years, were treated as independent samples for statistical purposes.

Photographic analysis

The content of the camera memory cards was downloaded to a laptop every two to eight months. The daily videos were transformed into individual photographic frames in JPG format using Brinno Video Player software (<https://www.brinno.com/support/download>). Under this conversion, 54 photographs were obtained per day. In the first photograph, the nests to be analyzed were identified and

numbered; there were usually 20–70 nests within a flat colony and 17–25 nests in cliffs. Once selected and numbered, the nests were inspected in each photograph until the date of definitive nest desertion or fledging. Using this method, it was possible to obtain the daily percentage of abandoned nests (abandoned nests/d/total number of inspected nests $\times$ 100) and, consequently, the cumulative percentage of nest desertions during the colony monitoring period. In total, the monitoring of all studied nests (five colonies, 256 nests) required approximately 250–300 effective hours of analysis (in real time, four analysis h/d was equivalent to 63–75 d).

The intensity of ectoparasite infestation in birds was measured indirectly through observation of bird behavior in each photo. When faced with a significant load of ectoparasites or hyperinfestation, birds are known to spend more time scratching their legs, standing on the side of the nest, and/or preening themselves (Duffy 1983b). Thus, to quantify the occurrence of tick hyperinfestation, bird behavior was recorded for each nest site at 4-h intervals according to the following categories: seated on nest without preening (SE), seated on nest preening body (B), standing on nest or nest side without preening (ST), standing preening legs (STL), standing on nest preening body (STB), lying and preening legs (L), and absence of parents in the nest leaving its contents exposed (NP). For this behavioral assessment, only photographs taken at 06h00, 10h00, 14h00, and 18h00 were considered. Behaviors classified as STL, STB, or ST were considered “uncomfortable.” To calculate the proportion of birds in a state of discomfort, the number of nests containing one of the two adults in any of the three discomfort categories was divided by the total number of nests observed and then multiplied by 100. For example, in a photograph taken at 10h00, five birds exhibited STL, STB, or ST, while the behavior of 55 birds were classified into other categories. Thus, the percentage of discomfort was $5/60 \times 100 = 8.33\%$. To calculate this percentage per day, we proceeded in the same way, but the total occurrence of

discomfort at the four selected times was added and divided by the total number of behaviors in that day. It is assumed that in the case of a tick infestation, the proportion of birds in a state of discomfort will increase according to the intensity of the infestation.

To evaluate changes in the frequency of bird discomfort according to the time of day (06h00, 10h00, 14h00, and 18h00), data from Macabí Island were excluded because the camera lens was cloudy at 06h00 and 18h00 on a few days (the lens was exposed to the wind). Using these data could have led to an overestimation of the values for the other hours of the day.

Number of ticks in guano

To determine the level of tick infestation in recently abandoned colonies, 500-mL guano samples were collected outside and inside the booby colonies on Guañape Norte, Mazorca, Chinchá Sur, and Ballestas Norte islands in 2017. At each collection zone, two samples were taken outside and two samples inside the colony. On Chinchá Sur and Ballestas Norte islands, nest abandonment events and nests containing chicks aged 1.5 mo were also recorded, respectively. Samples were collected 2–16 wks after nest desertion and stored in Ziploc bags, then transported to the Unidad de Investigación de Ecosistemas Marinos of Universidad Científica del Sur for the identification and counting of adults and nymphs. It was assumed that the tick species in the guano samples of the booby colonies was *O. amblus* because it is the only tick species reported to date that parasitizes guano birds (Nava *et al.* 2017).

Statistical analysis

To evaluate possible correlations between the cumulative percentage of nest abandonment and the percentage of birds in a state of discomfort, nonlinear regression fitted the data to an exponential

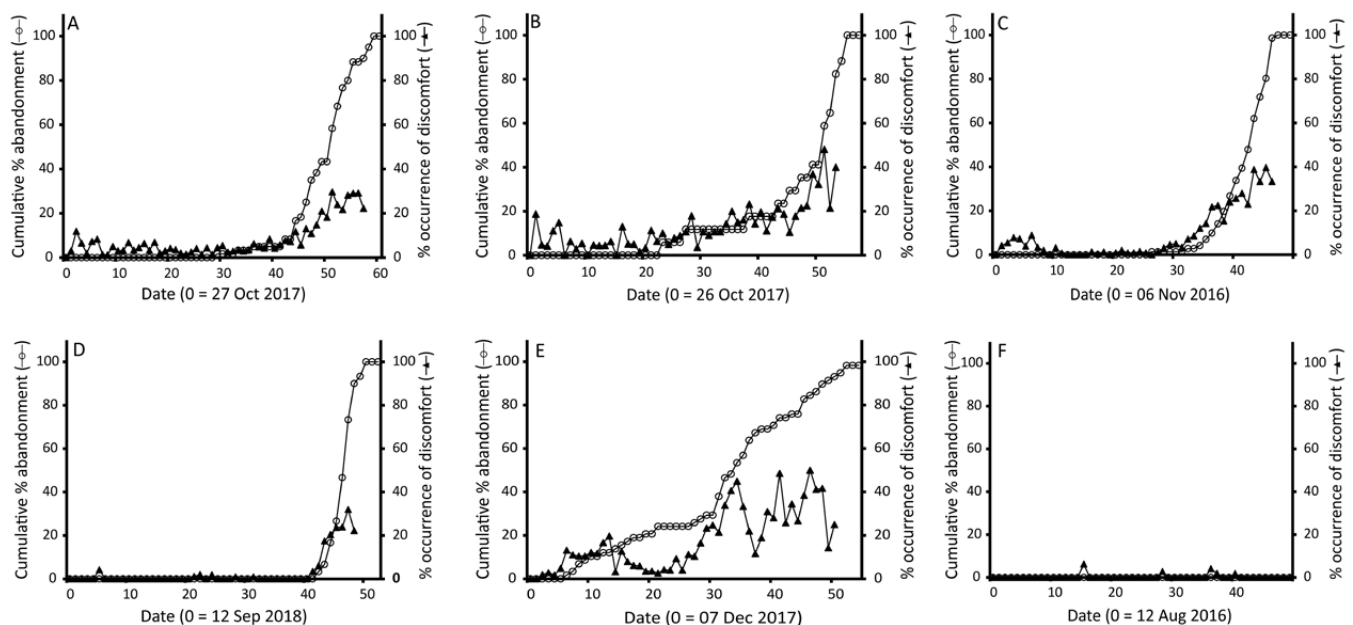


Fig. 2. Daily variation in the percentage of abandoned Peruvian Booby *Sula variegata* nests compared to the percent occurrence of bird discomfort (standing in the nest, standing and preening the body, or standing and preening the legs) on (A) Mazorca Island, water tank in 2017 ($n = 60$ nests); (B) Mazorca Island, kitchen roof in 2017 ($n = 20$ nests); (C) Guañape Norte Island, balcony in 2016 ($n = 71$ nests); (D) Guañape Norte Island, balcony in 2018 ($n = 30$ nests); (E) Macabí Island, house in 2017 ($n = 58$ nests); and (F) Punta San Juan, cliff in 2016 ($n = 17$ nests).

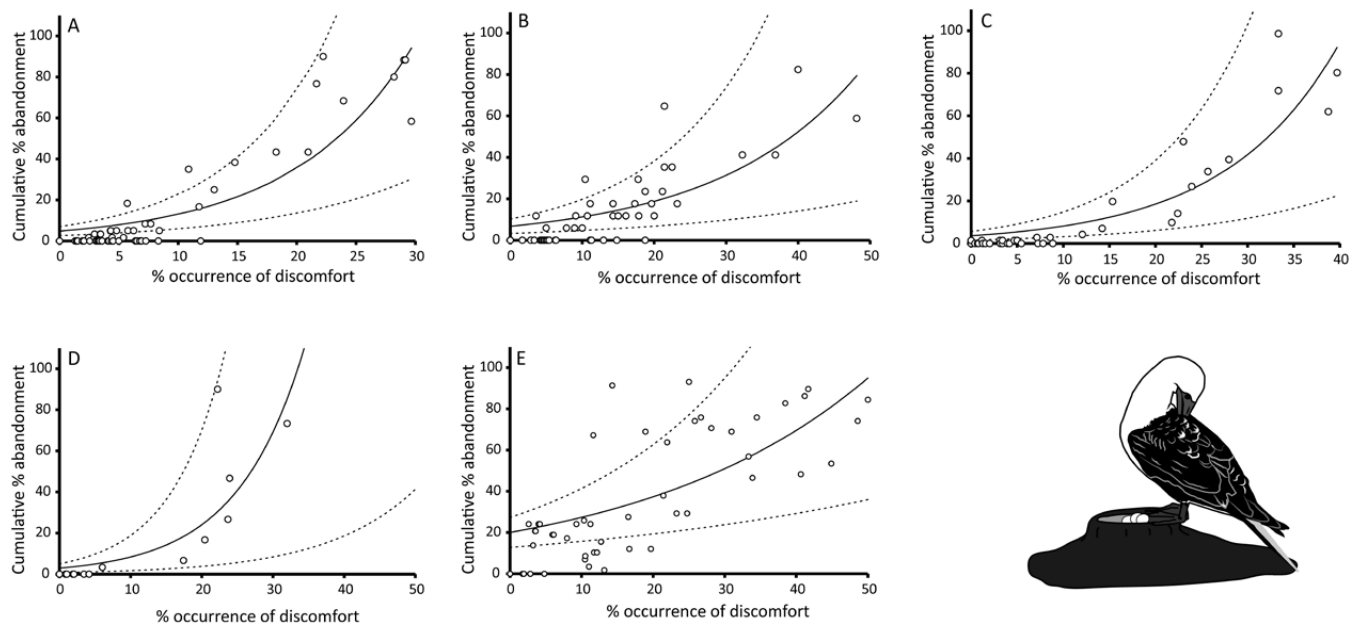


Fig. 3. Exponential relationship between the percent occurrence of discomfort and the percentage of abandoned Peruvian Booby *Sula variegata* nests: (A) Mazorca Island, water tank in 2017 ($n = 58$); (B) Mazorca Island, kitchen roof in 2017 ($n = 55$); (C) Guañape Norte Island, balcony in 2016 ($n = 47$); (D) Guañape Norte Island, balcony in 2018 ($n = 49$); and (E) Macabí Island, house in 2017 ($n = 52$). The data were fitted to an exponential equation ($y = a \times \exp(bx)$), represented by the solid line; the 95% confidence interval is represented by the dashed line.

equation ($y = a \times \exp(bx)$). General linear models (GLMs) were used to examine the effects of location and time of day on the percentage of birds in an uncomfortable state. Analysis of covariance (ANCOVA) was used to test whether the correlations between the cumulative percentage of nest abandonment and the percentage of birds in a state of discomfort varied among locations. For this purpose, logarithmic transformation was performed ($\ln(x+1)$) to linearize the data. The paired Student's *t*-test was used to compare the number of ticks inside and outside the colonies. The means are expressed ± 1 standard deviation (SD). The null hypothesis was rejected at a level of significance of $P < 0.05$. The statistical tests were performed using SAS 9.4 (SAS Institute Inc).

RESULTS

During the study period, sea surface temperature varied between 16–18 °C for the different study locations based on daily satellite monitoring of oceanographic parameters recorded by the Marine Institute of Peru (Instituto del Mar del Perú, IMARPE) (http://satelite.imarpe.gob.pe/uprsig/sst_prov.html).

Discomfort behavior and nest abandonment

Of the six events observed, five were abandoned during the incubation period (Fig. 2A–E), and only one (Punta San Juan) was successful (Fig. 2F), i.e., the chicks reached fledging age. During the first days of incubation, the photo log showed that the boobies stayed full-prone over their nests or groomed in this position. Less than 20% of the observed behaviors were discomfort behaviors in these first weeks, when no significant nest abandonment was observed (Fig. 2A–D). Nest abandonment occurred between 35 and 50 d after positioning the cameras. This abandonment occurred abruptly over an interval of two weeks (Fig. 2A–D);

however, on Macabí Island, the abandonment of nests was progressive (Fig. 2E). The percent occurrence of discomfort behaviors was exponentially correlated with the percentage of nest abandonment (Fig. 3A–E; $P < 0.0001$ for all tests). In the case of Punta San Juan (Fig. 2F), no discomfort behaviors were observed, nor were nests abandoned.

Effects of time of day and colony on the discomfort behavior of birds

During the nest abandonment phase (exponential phase of the cumulative abandonment curve, Fig. 2), the percentage of birds in a state of discomfort varied significantly according to the time of day, being generally greater at 10h00 (GLM, $F_3 = 4.01$, $P = 0.008$; Fig. 4). There were no significant differences in this percentage among colonies (GLM, $F_3 = 0.36$, $P = 0.36$; Fig. 4) or in the colony $\times$ time of day interaction (GLM, $F_9 = 1.23$, $P = 0.276$), indicating that the mean percentage of birds in a state of discomfort was similar among the colonies, varying between 12% and 32%. In contrast, when evaluating the relationship between the cumulative percentage of nest abandonment and the percent occurrence of discomfort, significant differences were found in the percentage of birds in a state of discomfort $\times$ colony interaction (ANCOVA, $F_3 = 18.02$, $P < 0.001$). This indicated that the correlation between the percentage of birds in a state of discomfort and the percentage of nest abandonment was different among the colonies.

Tick density

The density of ticks in deserted nests varied between 12 individuals/500 mL of guano on Guañape Norte and 321 individuals/500 mL of guano on Ballestas Norte (Table 1). There were significant differences in the density of ticks inside

(mean $\pm$ SD: 105.41 $\pm$ 92.8 ticks/500 mL of guano) and outside (43.08 $\pm$ 39.8 ticks/500 mL of guano) the colony (paired *t*-test, $t_{36} = 3.36$, $P = 0.0063$).

DISCUSSION

This study confirmed the findings reported by other researchers (LaValle 1923, Murphy 1925, Vogt 1942, Duffy 1983b) that tick *Ornithodoros amblus* infestation causes drastic changes in guano bird behavior and nest abandonment. Additionally, this study reveals, for the first time in Peru, that time-lapse cameras can be used reliably not only to estimate the reproductive success of boobies, but also to evaluate the causes of nest desertion.

Parasites are organisms with a wide distribution that possess the ability to control, regulate, and limit the abundance of their hosts. Likewise, they can regulate the structure of ecological communities by controlling key species in the trophic chain in top-down systems, and can even have a positive effect on biodiversity (Frainer *et al.* 2018). Ectoparasites, in particular, cause mortality in large groups of individuals, in some cases allowing the resources used by the hosts (food, habitat) to be available to other competing species. This ecological concept is crucial for understanding the role of ticks in guano bird populations and their possible effect

on new anthropogenic variables, such as fishery depletion of prey, pollution, disturbance, introduction of invasive species, and global warming, because these factors could increase the adverse effects of ticks on guano birds. For example, before human presence on the Peruvian coast, ticks could have been important regulators of guano bird populations amidst the proliferation of millions of guano birds in a highly productive environment such as the Humboldt Current system. However, at present, given the various anthropogenic factors mentioned above, the effect of ticks on population size could be much greater. This issue was so important that lizards were introduced into the guano islands as controlling agents for ticks for the benefit of guano birds (Vogt 1939, Pérez & Jahncke 1998).

In the guano islands of Peru, the effects of tick infestation on guano birds are considerable. It has been reported that the tick *O. amblus* has been the cause of mass abandonment of nests, with losses of between 500 000 and 750 000 eggs and chicks of the three species combined on Mazorca Island alone (Duffy 1983b). Duffy (1983b) suggested infestation levels were linked to time since last guano harvest. The harvest sweeps guano down to bedrock and then uses brooms that also remove the guano with ticks.

Tick density and abandonment of booby nests

This study found variations in tick density (number of adults and nymphs in 500 mL of guano inside colonies) ranging from 12 ticks on Gualaípe Norte Island to 321 ticks on Ballestas Norte Island. These densities are similar to or higher than those found in abandoned booby colonies from other islands of the Peruvian coast (mean of 1–52 ticks in 500 mL of guano; Duffy 1983b). In the case of booby nest abandonment on Gualaípe Norte Island in 2017, the density of ticks was 79 individuals, while in 1978 on the same island, the density was 52 individuals (Duffy 1983b). Thus, these ectoparasite densities are typical of booby colonies that have been recently abandoned. When areas inside and outside of recently abandoned colonies were compared, significant differences were found in the density of ticks, including higher values in booby colonies, where up to 75% abandonment was recorded (Duffy 1983b). This finding shows that nest abandonment was associated with tick infestation. Duffy (1983b) recorded higher tick densities in areas close to active nests. The highest density was found on Macabí Island, at 150 individuals (adults and stage three and four nymphs) in 500 mL of guano (Duffy 1983b). In the present study, the highest density was recorded on Ballestas Norte Island (321 ticks in 500 mL of guano). Ramos & Drummond (2017) noted

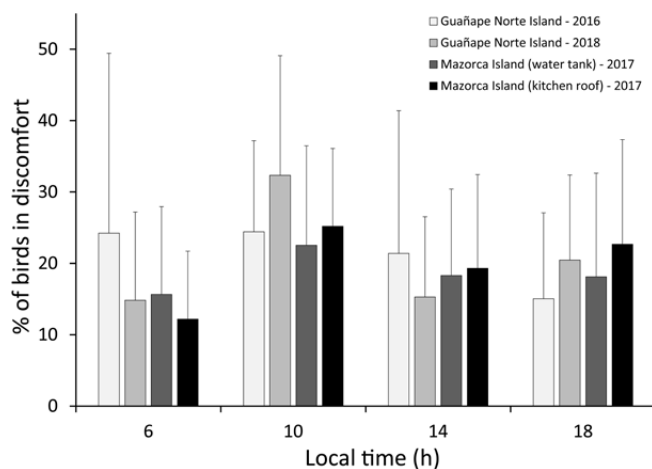


Fig. 4. Mean $\pm$ standard deviation of the percentage of birds with discomfort according to the time of day in four reproductive groups of Peruvian Booby *Sula variegata*.

TABLE 1
Tick density in 500 mL guano samples taken from inside and outside colonies in locations where there was desertion of Peruvian booby nests

Location	Date of collection	Date of desertion	Ticks inside the colony		Ticks outside the colony	
			Mean	Standard deviation	Mean	Standard deviation
Mazorca	Feb 2017	Dec 2017	68.5	17.7	18.0	7.1
Ballestas Norte	Jan 2017	Jan 2017	288.5	46.0	115.5	53.0
	Apr 2017	May 2017	122.5	20.5	51.5	10.6
Gualaípe Norte ^a	Jan 2017	Dec 2016	65.0	19.8	27.5	14.8
	Apr 2017	-	21.5	13.4	20.5	9.2
Chincha Sur ^a	Mar 2017	-	66.5	24.7	25.5	12.0

^a No nest desertion recorded

that the numbers of the tick *Carios denmarki*, an ectoparasite of the Blue-footed Booby, has a close relationship with nest density. Of the areas that they evaluated, the chicks in areas with a high nest density had a greater number of ticks, while the areas with a low density of nests had a low abundance of ticks. Likewise, other studies indicated that ticks may have a certain preference for rocky habitats (LaValle 1923, Vogt 1942, Iannaccone & Dale 1997, Ramos & Drummond 2017), characteristics that coincide with Ballestas Norte Island. The area where the guano sample was collected in this study was characterized by having an irregular surface, with a large number of rocks and was very close to a reproductive subcolony. Such conditions would provide ticks with food and shelter.

Discarding other nest desertion factors

The photographic analysis allowed us to discard other factors that could cause nest desertion in Peruvian Boobies, such as unexpected disturbances in the colonies. Likewise, predation effects were ruled out because the time-lapse cameras did not record the presence of predators, and in many of the records, the entire contents of the nests were observed once the parents deserted. One factor that has a strong influence on nest abandonment is an anomalous increase in sea surface temperature, which would have been related to decreased prey availability, but this was not observed during the study period.

Effectiveness of time-lapse cameras

In this study, time-lapse cameras allowed the identification of a change in behavioral patterns in the boobies that occurred at different times of day and throughout their reproductive period. The use of this technology represents a great advantage for researchers because it significantly reduces the time spent in the field and the costs required to remain on the islands during the extensive reproductive period (5–6 mo for the Peruvian Booby; Nelson 1978). It also allows researchers to obtain information simultaneously on different reproductive variables of guano birds in different locations. However, when using time-lapse cameras, it is important to consider the time that is required to perform the photographic analyses. In this study, data from six locations from 2016 to 2018 were analyzed, which took approximately 250–300 h. It is expected that in the coming years, with the advent of machine learning, the time needed for photographic analysis will be considerably reduced, making time-lapse cameras a practical tool for use on the guano islands. Another important limitation that should be considered is the blurred visibility produced by moisture, wind, and soil, which caused images from some locations to be blurred, making photographic analyses difficult and in some cases impossible.

CONCLUSIONS

Time-lapse cameras are good tools to monitor the reproductive success of seabirds and can also provide details of the causes of mortality through observation of changes in seabird behavior in photographs. Using these cameras, we were able to determine that ticks cause mass desertion of Peruvian Booby nests in different colonies. This use of time-lapse cameras could also be applied to the study of other seabird species of the Peruvian coast and to analyze other factors that cause nest desertion, such as the presence of predators, human disturbance, and other factors that the cameras can record. Future studies should evaluate the abiotic and biotic conditions that ticks require for their development, such

as habitat type and environmental temperature, and should also examine the microclimates, interactions with predators, and other variables that explain their high densities on guano islands and headlands, including their interaction with and effect on guano bird populations.

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