# USE OF AN HONEST SIGNAL BY RED-FOOTED BOOBIES *SULA SULA* IN RESPONSE TO KLEPTOPARASITISM BY GREAT FRIGATEBIRDS *FREGATA MINOR*

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## ABSTRACT

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On Genovesa Island (00.3°N, 089.9°W) in the Galápagos Islands, Ecuador, Great Frigatebirds *Fregata minor* kleptoparasitize (i.e., steal food from) Red-footed Boobies *Sula sula*. In five of eight cases that I observed, the frigatebirds harassed the boobies until the latter regurgitated their forage, which the frigatebirds consumed. In three cases, the booby responded with a honk-like call and the frigatebirds stopped harassing. I propose that the honk is an "honest signal" by a booby having little food to divulge. Boobies loaded with forage do not honk because the call could trigger regurgitation. Thus, frigatebirds harass with escalation only non-honking boobies. The interaction is important in what appears to be a food-limited booby population.

**Key words:** food limitation, Galápagos, honest signals, kleptoparasitism, vocal displays

Birds use signals, most often acoustic and visual, for a variety of intra- and inter-specific interactions. Signals can be used to attract a mate, repel a competitor, or discourage a predator, with the meaning of the signal being dependent on the context (Bradbury & Vehrencamp, 1998). Because the sender and the receiver of the signal can gain or lose depending on the outcome, the signal can be analyzed for its "honesty" (Bradbury & Vehrencamp, 1998; Searcy & Nowicki, 2005; Zollman et al., 2013). An honest signal would be unfakable and not deceitful (Chisausky et al., 2023). For example, after detecting the presence of a predator, birds can emit warning (alarm) calls, which are generally attributed to two explanations. First, the call could protect the flock, whether there is a kinship or not, by advertising the presence of danger (Leavesley & Magrath, 2005). Second, the sender is communicating that it is prepared to fend off the predator, and thus the predator would be better off focusing on an individual that is unaware of its presence (Randler, 2016). Note that regardless of which explanation is correct, the alarm signal needs to be honest. Honest signals have been postulated for other behaviors, including mate choice and manifesting vigor (Velando et al., 2006), aposematic (warning) coloration (Hedley & Caro, 2022), and nestling begging (Villaseñor & Drummond, 2007). However, signals can also be dishonest or deceitful. For example, alarm calls could have a dishonest component, such as when used in the absence of predators to scare away other individuals to minimize local competition (Flower et al., 2014; Møller, 1988; Munn, 1986; Ridley et al., 2007). Given the recent rise in criticisms of honest signals (Chisausky et al., 2023), novel examples would be desirable, as they could provide additional perspectives.

On 01 May 1993, I had the opportunity at Darwin Bay on Genovesa Island in the Galápagos Islands, Ecuador (00.3°N, 089.9°W), to observe interactions between Red-footed Boobies *Sula sula* and Great Frigatebirds *Fregata minor* that could provide a novel example of honest signals. Because Genovesa is one of the more remote islands of the archipelago and overnight stay is not permitted, the time window and sample size for my observations were small. Nonetheless, a search of the literature from the last 30 years has not revealed any findings similar to my observations. Thus, I present here my results to make the case for a novel example of an honest signal.

My observations on Genovesa noted that Red-footed Boobies returning from foraging were kleptoparasitized by Great Frigatebirds, which had been guarding the shoreline and entry to the island. The kleoptoparasitism consisted of the frigates harassing the incoming boobies on the fly by physical contact, including pulling feathers, until the latter regurgitated the prey they had acquired (most likely flying fish (Exocoetidae); Nelson, 1969a), which was then consumed by the frigate.

Kleptoparasitism could adversely affect the Red-footed Boobies in Genovesa population. Previous studies, which are still the most detailed, have shown that the booby's natural history and annual cycle on Genovesa is characterized by erratic and scarce food supplies, unlike populations elsewhere (Nelson, 1969a, 1969b). The island's population of Red-footed Boobies is one of the largest in the world (140,000 breeding pairs in the 1960s; Nelson, 1969b). Egg incubation at this site takes 45 days on average. Because of food scarcity, chick growth is slow, and parents must feed their chicks over 200 days. As a result, individuals can breed only once every two years. In other parts of the world, Red-footed Boobies breed annually (Nelson, 1969a). Because food availability also appears to be erratic, breeding is asynchronous without any peak month; 70% of eggs are lost and 72% of chicks perish before fledging (Nelson, 1969a). Egg loss is largely due to nest desertion by the incubating parent when the foraging parent fails to return in time with food.

Kleptoparasitism could therefore contribute greatly to the loss of both eggs and chicks. A more recent study of Genovesa's Red-footed Boobies (Mendez et al., 2017) concurred that the estimate of 140,000 pairs (Nelson, 1969b) remains the best assessment of the population size. They also reported that the duration and range of booby foraging trips averaged 37 h and 176 km (and lasted up to five nights and 472 km). The study also showed that the population size, duration, and range values were among the highest compared to other Red-footed Booby colonies, which reaffirms the severity first described by Nelson (1969a, 1969b) for the conditions experienced by the birds on Genovesa.

I was able to observe a total of eight cases, and in close enough proximity to record the interactions between the booby entering and exiting the area guarded by the frigates (Table 1). In five cases, the entering booby was approached by one or more frigates and was harassed until it regurgitated. The harassment could escalate from the approach to bodily contact and the pulling of feathers, but the regurgitation ended the escalation. In three cases, the booby reacted to the approaching frigates by opening its beak to a wide gape, as if emitting a call, in which case the frigates ended the harassment and allowed the booby to fly through without interference. The behavior was a striking behavior that visually resembled a "honking," although no vocalization was heard because the booby was too distant. The honks also appeared to be directed at the frigates. In one of the three honking events, the booby was observed to regurgitate as soon as it honked, as if the act of honking had triggered the regurgitation.

My results revealed a clear negative correlation between honking and escalation (Table 1; Pearson's correlation coefficient of $r = -1$). Because of the small sample size of the data, a chi-square test could not be used to assess the significance of the correlation. Thus, I used a randomization test to determine the probability of obtaining a value of $r$ smaller than or equal to $-1$ by a null model that serves as the alternative hypothesis that honking and escalation acted independently (i.e., are not correlated). A randomization test makes no assumption about the underlying distribution of the data and, therefore, is not biased by small sample sizes (Manly, 2018). The randomizations rejected the null model ($P = .0189$; Table 1). Thus, honking and escalation between boobies and frigates in my study were negatively correlated and not acting independently.

The fact that boobies can avoid or stop harassment by the frigates by honking raises two questions. First, why do boobies not honk more often or all of the time to protect themselves from kleptoparasitism? Second, why do frigates respect honking? In other words, why is the negative correlation I observed not broken by either of the two birds? I propose that all of these questions are addressed if honking is an honest signal reporting that a booby had no or very limited forage stored in its upper digestive track. The signal could be honest, or unfakeable (Chisausky et al., 2023), if honking was physiologically demanding, such that a booby could not give a loud honk and retain a full load of prey at the same time. A sufficiently loud honk would trigger the regurgitation of the forage. Thus, frigates respect a loud honk because a honking booby has little or no forage to give. In turn, boobies honk because that frees them from escalating harassment. Finally, boobies with a full load of forage do not honk because they will regurgitate, which is the outcome desired by the frigates. The lower limit for what is a sufficiently loud honk will be controlled by the frigates, either through evolution or by learning, so that the signal remains honest by triggering regurgitation. The upper limit is determined by the boobies, which do not want honking to be too energetically costly when they have little or no forage.

I recognize that my demonstration of a negative association between honking and harassment, although statistically significant, does not confirm that honking is an honest signal. I am only proposing the honest signal as a hypothesis. I have noted that only one of the observed boobies regurgitated as it honked. While this is one observation is not replicated, I used it to motivate the hypothesis, because it appeared to me that the honking triggered the regurgitation. I considered an alternative hypothesis that honking was a warning given by the boobies before fighting the harassing frigates. The fight back rendered the signal honest rather than a bluff. However, because boobies were not observed fighting back, the hypothesis was not further examined.

**TABLE 1**
**Observations of honkings by Red-footed Boobies *Sula sula* and escalations of harassment by Great Frigatebirds[a] *Fregata minor* on Genovesa Island in the Galápagos Islands, Ecuador, in May 1993**

| **Observation** | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| **Honk** | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| **Escalation** | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |

[a] Data are for eight observations and were not collected in the order presented. For illustration, Observation 1 noted that the booby honked and the frigate did not escalate. Because all honks led to no-escalation and all no-honks to escalation, honking and escalation were perfectly corrected and the observed Pearson's correlation was $r_{Obs} = -1$. Although the statistical assumptions underlying $r_{Obs}$ may not be satisfied by the binary data, Pearson's $r$ was used only as a proxy for the correlation in a randomization test that did not rely on the assumptions. To determine whether $r_{Obs} = -1$ was statistically significant, the randomization test estimated the distribution of $r_{Null}$ or the correlation resulting from the null model (hypothesis) that honking and escalation acted independently. At the $P = .05$ level, $r_{Obs} = -1$ would be statistically significant if less than 5% of $r_{Null} = -1$. The randomization test was accomplished computationally in R (R Core Team, 2021). I first let the vectors $H_{Obs} = \{1,1,1,0,0,0,0,0\}$ and $E_{Obs} = \{0,0,0,1,1,1,1,1\}$ denote the observed data for honking and escalation. A single estimate of $r_{Null}$ was obtained by measuring the correlation between a shuffled $H_{Obs}$ and a shuffled $E_{Obs}$. The shuffling consisted of sampling with no replacement the contents of each vector, e.g., a shuffled $H_{Obs}$ could be $\{0,0,1,0,0,1,1,0\}$, but it always contains three 1s. A total of 10,000 $r_{Null}$ values were generated and tallied. An $r_{Null} = -1$ was randomly generated 189 times, in which case the probability that $r_{Obs} = -1$ could have arisen by chance from the null model is 189/10,000 or $P = .0189$. Thus, the observed correlation honking and escalation is statistically significant at the .05 level.

Honest signals have been documented in Blue-footed Boobies *Sula nebouxii*, in which feet coloration is an honest signal to females for the caloric health of males (Velando et al., 2006) and begging by chicks honestly reflects the need for food (Villaseñor & Drummond, 2007). More information on Red-footed Boobies is needed to determine whether honest signaling helps them thwart kleptoparasitic frigatebirds. It would be desirable to know if boobies return from foraging with a gradient of fullness, whereby boobies below a fullness threshold can honk and not regurgitate. The one honking/regurgitating booby I observed could have been at the threshold and have equally regurgitated or not. I hope that the Red-footed Boobies on Genovesa will be targeted by future studies. Because the two-year breeding cycle of these boobies is unique to the island (Nelson, 1969a) and may have resulted from interference by the frigates, the use of an honest signal in response to kleptoparasitism could also be unique to Genovesa.

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