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Hormones and Behavior 43 (2003) 402–407

Hormones
and Behavior

www.elsevier.com/locate/yhbeh

Correlation between plasma steroids and chick visits by nonbreeding adult Nazca boobies

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Received 3 October 2001; revised 3 May 2002; accepted 28 October 2002

Abstract

Nonbreeding adult Nazca boobies (*Sula granti*) often approach unattended chicks and perform parental and/or aggressive behaviors toward the chicks. Earlier descriptions of these encounters included sexual behaviors as well. We studied hormonal correlates of chick visits by such nonbreeding boobies during the breeding season. We compared the hormonal status of chick-visiting adults with that of nonvisiting adults in the colony. We determined levels of corticosterone (CORT), testosterone (T), androstendione, dihydrotestosterone, and estradiol as potential candidate hormones controlling parental, aggressive, or sexual behavior. Only T and CORT differed between chick-visiting and nonvisiting adults. Chick-visiting adults had higher CORT levels after the interaction than nonvisiting adults randomly caught in the colony. To the contrary, T levels after interactions were lower in chick-visiting compared to random nonvisiting adults. T levels, however, did not vary with level of aggression among chick-visiting adults. We suggest that chick-visiting behavior may be permitted by low T levels and activated by, or resulting in, high CORT levels.

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Keywords: Nazca booby; *Sula granti*; Testosterone; Corticosterone; Galápagos; Seabird; Hormones

Introduction

Nazca boobies (*Sula granti*) are ground-nesting, monogamous seabirds that breed colonially on oceanic islands. Chicks are typically attended by a parent continuously during the first 25 days after hatching. At ~25 days, chick body mass reaches ~500 g and its increasing food demands require both parents to be absent from the nest simultaneously to forage (Anderson, 1990; Anderson and Ricklefs, 1992). When chicks are left unattended they are often approached by other adults on the colony, which we call “nonbreeding adult visitors” (NAVs). NAVs may simply stand or sit next to the chick, but typically they perform a combination of parental, aggressive, and/or sexual behaviors toward the chick (Anderson, D.J., unpublished data). Parents invariably chase the NAV from the nest if one is

present when they return from foraging trips (personal observation). Chicks usually adopt a submissive “bill-hiding” posture (Nelson, 1978) during these visits, in which the bill is pressed against the chest and the back of the neck is exposed. This posture may reduce the severity of NAV aggression (Nelson, 1978). Serious aggressive encounters can cause abrasions and lead to the death of chicks through subsequent blood feeding by land birds (Curry and Anderson, 1987; personal observation).

Nelson (1978) first described the behaviors exhibited by nonbreeding adults as males approaching chicks and attempting to copulate with them. In these encounters, the chicks did not facilitate the copulation and the NAVs then attacked the chicks aggressively (Nelson, 1978). In the current study, we analyzed the hormonal status of NAVs during these visits, focusing on the proximate regulation of NAV behavior. Testosterone (T) and related androgens are often involved in aggressive and/or reproductive behaviors of vertebrate animals, and many bird species have high

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Table 1
Levels of aggression exhibited by 61 nonbreeding adult visitors (NAVs), description of behavior, and percentage of total NAVs exhibiting the level of aggression

Level of aggression	Description of behavior	Percentage
Low	Gentle and very infrequent biting, no shaking or pulling out feathers, no wounds created	58.3
Medium	Biting, no shaking or pulling out feathers, no open wounds created	20
High	Biting, infrequent shaking and pulling out feathers, sometimes leading to open wounds	15
Extreme	Vigorous shaking, biting, and pulling out feathers, leading to large open wounds and often the death of the chick by subsequent blood feeding by land birds	6.7

levels of circulating sex steroids during times of aggression and breeding (Hau et al., 2000; Wingfield et al., 1990). Additionally, corticosterone (CORT) levels can increase in response to stress of various kinds (Harvey et al., 1984; Romero et al., 1997). CORT has also been shown to increase in anticipation of stressful events (Lupien et al., 1997; Ramade and Baylé, 1986). We investigated the T levels of NAVs exhibiting different levels of aggression, and compared levels of CORT and T for NAVs versus random individuals in the colony that did not visit chicks (non-NAVs). We hypothesized that aggressive and/or sexual behaviors by NAVs could be activated by increased plasma T levels: T levels of NAVs should be positively correlated with indices of aggressive or sexual behavior. It is unclear, however, if NAVs should be expected to have higher T levels than non-NAVs, because non-NAVs also engaged in sexual and aggressive territorial behaviors around the colony. We further expected NAVs to experience stress associated with occupying a territorial breeder's nest site, or have a direct stress response from interacting with a foreign chick. Each could result in high plasma CORT levels. Thus, NAVs should have higher CORT levels than non-NAVs. Additionally, we hypothesized that the levels of other androgens such as dihydrotestosterone (DHT) and androstendione (A4) would be elevated in NAVs exhibiting high levels of aggressive or sexual behaviors. Estradiol (E2) was analyzed because it could increase with aggressive or sexual behaviors of female NAVs in particular (Schlinger et al., 1992).

Materials and methods

Field

We studied Nazca boobies at Punta Cevallos, Isla Española (89°37'W, 1°23'S) in the Galápagos Islands during January 2000. Continuous observations by D.J.A.'s field crew also covered the entire time between October 1999 and June 2000. We used behavioral observations during this time period to exclude the possibility that any NAVs were wrongly characterized as nonbreeders during the shorter field season when hormone levels were investigated. Nazca boobies were formerly considered a subspecies of masked boobies (*Sula dactylatra granti*), but recent analyses of

morphological and breeding data (Pitman and Jehl, 1998; Roberson, 1998) and of mtDNA differentiation (Friesen et al., 2002) support the taxon's elevation to species status (American Ornithologists' Union, 2000). Total population size at our study site is about 10,000 individuals. We conducted focal observations of adult Nazca boobies that approached unattended chicks at foreign nests. If these adults interacted with the chick they were termed "NAVs" (i.e., the adult had to approach and interact with the chick on or near the chick's nest site to be considered a NAV; interactions never occurred on any other birds' nest site/territory). NAV-chick interactions were observed opportunistically as long as possible: at times we observed the interaction entirely, at times we began our observations after an interaction had already begun, and at times interactions were stopped short due to human intervention for blood sampling. Observations were at least 5 min in length and made from a distance of at least 10 feet from the nest site so that observations did not interfere with the birds or alter their behavior. Additionally, individuals in the study colony are almost entirely fearless and used to months of observer presence per year for many years. Therefore, we do not expect any observer influence on baseline CORT levels in our study. During the interaction we noted the following: nest site, sex of NAV, level of aggression exhibited by the NAV (aggression levels were categorized according to the behaviors exhibited during the NAV/chick interaction, see Table 1) and whether the NAV was single or acted as part of a pair. We also noted any physical contacts between the adult and the chick, including copulation attempts, aggressive biting, or preening. NAVs were captured for blood sampling toward the assumed end of the interaction with the chick, or immediately following the interaction. Because NAVs had to be captured before they flew off the nest, at times we interrupted the visit and thus could not unequivocally quantify the exact duration of all NAV/chick interactions. Therefore, we did not use "duration of visit" in any inferential statistical analysis. Non-NAVs were randomly chosen nonbreeding adults not visiting chicks at the time of capture and were not observed to have visited chicks over the course of this study. None of these non-NAVs were birds that were breeding, or had previously bred, in the study colony during the entire reproductive season. Therefore, we consider our sample of non-NAVs as an adequate comparison group to the equally nonbreeding NAVs that were visiting foreign chicks. The

non-NAVs that were blood sampled were not seen acting as NAVs at any time throughout this study.

Both NAVs and non-NAVs were sampled at similar times throughout the month-long study. Non-NAVs (as mentioned above for NAVs) were also observed for at least 5 min from a distance of at least 10 feet. Individuals were captured and carefully removed from the nest site for blood sampling. Blood samples were obtained by puncturing the superficial brachial wing vein with a 26-gauge needle. Blood was collected in heparinized microcapillaries (300–600 μ l) within 5 min and all samples used for CORT analysis were collected within 3 min of initial approach to prevent any capture and handling influence on CORT levels (see Wingfield and Farner, 1976). Individuals were weighed in a bag with spring scales. We then sprayed a small dot of black spray paint on the back of the head of each captured individual before release, to ensure that each individual was sampled only once. The sex of adults was determined by sex-specific vocalizations (Nelson, 1978). The sex of the chicks was not determined.

Plasma was separated by centrifugation (at 588×10^2 m/s for 4 min), removed, and treated with 10 μ l of B-propiolactone to destroy viruses, according to US import regulations for avian blood. Plasma was then stored in ethanol and transported to the University of Illinois and stored at -20°C until hormone analysis. The use of alcohol as the initial method of steroid hormone preservation had been validated prior to our investigations (Hau, M., Wikelski, M., unpublished data).

All NAVs observed were used in this study, totaling 60. Due to capturing difficulty, only 28 individuals were sampled for hormone analysis (18 males, 9 females, and 1 of unknown sex), and marked after capturing and blood sampling. We could not get a blood sample for CORT (< 3 min) from 1 male, reducing the sample size for CORT in males to 17. None of these marked NAVs were observed again during the study; thus, we assumed that the remaining 32 unmarked (not captured) NAVs for which we have behavioral observations were separate individuals, precluding pseudoreplication in our data set. Fourteen randomly chosen non-NAVs were sampled for hormone analysis (8 males and 6 females). We could not get a blood sample for CORT (< 3 min) from 3 males and 3 females, reducing the sample sizes to 5 males and 3 females for CORT.

NAVs are typically young, prebreeding adults, or breeding age adults that have no offspring when they exhibit NAV behavior (Anderson D.J., unpublished data). Nine of the 28 NAVs captured for blood sampling were banded individuals used for long-term census analysis and these NAVs had not bred at all during or prior to the 1999–2000 breeding season. We excluded one adult from the analysis that appeared to be a parent aggressively interacting with her own chick. This individual apparently attacked the chick without recognizing it as her own because the chick was at least 3 feet off of its nest site, after it was badly attacked by

a NAV and forced to run away from blood-feeding mockingbirds and finches.

As with 19 of the NAVs, none of the non-NAVs were banded individuals and therefore we were unable to compare individuals of different ages, which could have an effect on hormone levels. However, CORT apparently does not vary with age in Nazca boobies (Tarlow, E.M., unpublished data).

Behaviors exhibited by NAVs toward chicks included a combination of aggressive behaviors such as biting (often the neck, wings, or posterior), shaking (the NAV held the chick's neck with its beak and shook the chick by the neck), stepping and standing directly on the chick, pulling out feathers, and parental behaviors such as preening the chick and protecting it from other NAVs; the latter was similar to territorial behavior. Other behaviors regularly seen at the nest site included nesting behaviors, where the NAV picked up nest materials at the site. NAVs also displayed courtship behaviors, either between two NAVs at the site (in the case of a pair) or one NAV (male) trying to attract another individual (female) to the nest site.

Research conducted during this project was permitted under the regulations of the University of Illinois, Urbana-Champaign Office of Laboratory Animal Research, and adheres to NIH standards for the use of animals in research.

Laboratory analysis

Plasma levels of T, DHT, A4, E2, and CORT were determined by radioimmunoassay after separation of hormones on a chromatography column (e.g., Wingfield and Farner, 1975; T and DHT antibody: T3003, Wien Laboratories, Succasunna, NJ; CORT antibody: B3-163 Endocrine Sciences, Calabasas, CA; A4 antibody: AN6-22, Endocrine Sciences; E2 antibody: #1702, Biogenesis, Brentwood, NH). One NAV A4 sample, as well as one non-NAV A4 and DHT sample, were spilled during the assay, reducing the sample size for A4 in males to 17 and 7, respectively, and the sample size for DHT in male non-NAVs to 7. Blanks were below detection limit. Accuracy of the hormone standards was 6% for T and 9% for CORT. Assay sensitivity was at 0.05 ng/ml for T, 0.18 ng/ml for DHT, 0.25 ng/ml for A4, 0.2 ng/ml for E2, and 2 ng/ml for CORT. Intraassay variation was, on average, 6.7%. Our samples included positive controls; thus, low hormone levels in NAVs are true effects and not due to problems in assay procedures (see also Lormée et al., 2000, and Wingfield et al., 1999, for low hormone levels in boobies).

Statistical analysis

Data were processed and analyzed with SPSS for Windows (SPSS Inc., Chicago, IL). The four levels of aggression were ranked as follows: 1, low; 2, medium; 3, high; 4, extreme. Mann-Whitney *U* tests were used for two-sample comparisons and Kruskal-Wallis analyses of variance were

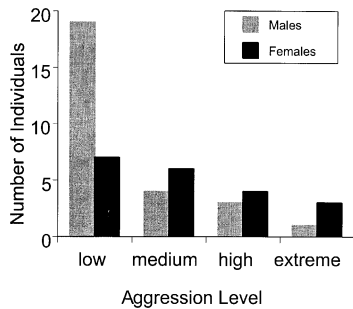


Fig. 1. The number of male and female nonbreeding adult visitors showing each level of aggression. See Table 1 for description of aggression levels.

used to make κ sample comparisons. Undetectable hormone levels were set at the lower detection limit. Significance of tests was accepted at the $\alpha = 0.05$ level.

Results

Visits by NAVs lasted from a few seconds to over 7 h, with short interruptions (median visit = 8 min). NAVs left the nest site when they were chased off by another adult (another NAV, a neighbor, or a returning parent), or when they apparently lost interest in the chick. Of the 60 NAVs observed during this study, 27 were male (45%), 20 were female (33.3%), and sex was not determined for the remaining 13 individuals (21.7%) because birds did not vocalize; 48.3% acted as a pair (pairs were always one male and one female), 43.3% were single, and 8.4% were both single and in a pair during the interaction. Individuals that were both single and in a pair during the event included one NAV that approached the nest in a pair and finished the event alone, and four other NAVs that approached the nest alone but were joined by another bird and finished the event in a pair. Three of these five NAVs were males that approached the nest alone and attracted females to the nest site with courtship displays.

Of the 60 NAVs observed, levels of aggression exhibited by NAVs ranged from low to extreme, with low levels of aggression common and extreme aggression rare (see Table 1). The level of aggression assigned to a NAV was based on the overall aggression level displayed by the NAV and aggression level did not vary within a NAV-chick interaction. Sexual behavior exhibited by a NAV toward a chick was only observed one time during this study and therefore only aggression was analyzed in detail.

No significant differences were found between individuals in pairs and single NAVs in the level of aggression exhibited (Mann-Whitney $U = 314.5$, $n = 29$ individuals in pairs, 26 single, $P = 0.245$). Overall, however, females exhibited higher levels of aggression than males (Fig. 1; Mann-Whitney $U = 170$, $n = 20$ females, 27 males, $P = 0.017$).

Hormone levels

Male and female NAVs did not show significant differences in hormone levels (T: Mann-Whitney $U = 78.5$, $n = 9$ females and 18 males, $P = 0.860$; CORT: Mann-Whitney $U = 62$, $n = 9$ females and 17 males, $P = 0.434$; DHT: Mann-Whitney $U = 76.5$, $n = 9$ females and 18 males, $P = 0.764$; A4: Mann-Whitney $U = 52.5$, $n = 9$ females and 17 males, $P = 0.171$). In addition, individuals in pairs and single NAVs did not show significant differences in hormone levels (T: Mann-Whitney $U = 75$, $n = 13$ individuals in pairs, 15 single, $P = 0.149$; CORT: Mann-Whitney $U = 66$, $n = 13$ individuals in pairs, 14 single, $P = 0.225$; DHT: Mann-Whitney $U = 83$, $n = 13$ individuals in pairs, 15 single, $P = 0.380$; A4: Mann-Whitney $U = 78$, $n = 12$ individuals in pairs, 15 single, $P = 0.468$). Among all NAVs we also found no significant relationship between hormone levels and aggression levels (T: Kruskal-Wallis, $\chi^2 = 2.318$, $df = 3$, $n = 28$, $P = 0.509$; CORT: Kruskal-Wallis, $\chi^2 = 0.269$, $df = 3$, $n = 27$, $P = 0.966$; DHT: Kruskal-Wallis, $\chi^2 = 0.779$, $df = 3$, $n = 28$, $P = 0.855$; A4: Kruskal-Wallis, $\chi^2 = 6.710$, $df = 3$, $n = 27$, $P = 0.082$; see Fig. 2 for T). No relationship existed between hormone levels and aggression levels within sex (males, T: Kruskal-Wallis, $\chi^2 = 1.450$, $df = 3$, $n = 18$, $P = 0.694$; males, CORT: Kruskal-Wallis, $\chi^2 = 1.977$, $df = 3$, $n = 17$, $P = 0.577$; males, DHT: Kruskal-Wallis, $\chi^2 = 2.262$, $df = 3$, $n = 18$, $P = 0.520$; males, A4: Kruskal-Wallis, $\chi^2 = 1.078$, $df = 2$, $n = 17$, $P = 0.583$; females, T: Kruskal-Wallis, $\chi^2 = 1.875$, $df = 3$, $n = 9$, $P = 0.599$; females, CORT: Kruskal-Wallis, $\chi^2 = 1.333$, $df = 3$, $n = 9$, $P = 0.721$; females, DHT: Kruskal-Wallis, $\chi^2 = 1.875$, $df = 3$, $n = 9$, $P = 0.599$; females, A4: Kruskal-Wallis, $\chi^2 = 2.08$, $df = 3$, $n = 9$, $P = 0.556$). However, we found significant differences in both T and CORT between NAVs and non-NAVs (Fig. 3; T: Mann-Whitney $U = 132$, $n = 28$ NAVs and 14 non-NAVs, $P = 0.037$; CORT: Mann-Whitney $U = 56$, $n = 27$ NAVs and 8 non-NAVs, $P = 0.041$). NAVs had higher

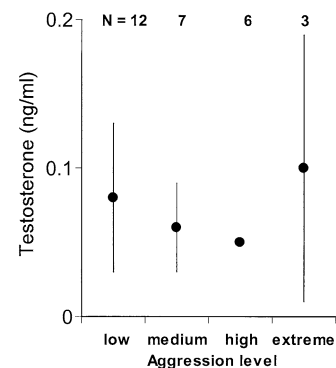


Fig. 2. Plasma testosterone levels of nonbreeding adult Galápagos Nazca boobies that interact with unattended chicks in a breeding colony (nonbreeding adult visitors). The aggression levels of adults were categorized from low to extreme, according to Table 1. Data show means and SE.

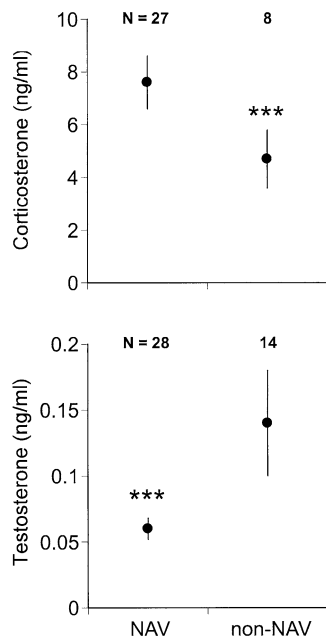


Fig. 3. Plasma testosterone and corticosterone levels of nonbreeding adult Galápagos Nazca boobies that interact with unattended chicks in a breeding colony (nonbreeding adult visitors, NAV) versus levels of adult nonbreeding birds (non-nonbreeding adult visitors, non-NAV). Data show means and SE. Stars indicate a significant difference.

CORT levels than non-NAVs (Fig. 3). To the contrary, NAVs had lower T levels compared to non-NAVs (Fig. 3). No significant difference was found between NAVs and non-NAVs in both DHT (Mann-Whitney $U = 177.5$, $n = 28$ NAVs and 13 non-NAVs, $P = 0.867$) and A4 (Mann-Whitney $U = 119$, $n = 27$ NAVs and 13 non-NAVs, $P = 0.065$). E2 was not detected in any sample and therefore was not analyzed.

Discussion

NAV behavior in Nazca boobies has previously been described as a sexually motivated behavior (Nelson, 1978), and copulation attempts have been observed during NAV visits to chicks (Nelson, 1978; Anderson, D.J., unpublished data; Wikelski, personal observation). During the current study we observed only one copulation attempt by a NAV toward a chick: the NAV approached the chick, tried to copulate, and then quickly departed the nest site. NAV behavior during our study consisted primarily of a combination of aggressive and parental behaviors exhibited by both male and female nonbreeding adults toward unattended chicks. Females were significantly more aggressive than males and thus female attacks may have been more likely to lead to the death of chicks through land-bird blood feeding (Curry and Anderson, 1987).

Plasma levels of steroid hormones appear to be generally low in adult boobies: T levels in masked boobies, formerly

considered the same species as Nazca boobies (Friesen et al., 2002), and red-footed boobies were close to detection limit except during the prelaying period (Lormée et al., 2000). Similarly, T levels in blue-footed boobies were very low and declined significantly from the egg-laying phase to the parental phase (Wingfield et al., 1999). Our analysis showed that T levels were also low in Nazca boobies, especially during NAV behavior. While NAVs were often aggressive, we did not detect elevated levels of T or related androgen levels with increased aggression levels. No relationship existed between aggression and T levels within each sex. We had no indication that other androgens (DHT and A4) or estrogens (E2) were correlated with NAV behavior.

Contrary to our prediction, NAVs had lower T levels than did non-NAVs. We suggest that NAVs may actually have low T levels because, hormonally, they are in the parental phase, even though they are not breeding at the time. Many NAVs displayed parental behavior toward the chick, in addition to showing aggression. We did not observe non-NAVs (equally nonbreeding) exhibiting parental behaviors; thus, we assume that none of these birds were in the parental phase. However, we cannot exclude the possibility that any of our non-NAVs may have exhibited aggressive behaviors around the colony, which in turn could account for their increased T levels compared to NAVs. However, due to our intense behavioral sampling effort, we consider this unlikely.

A similar situation (low T in more aggressive individuals) also exists in spotted hyenas (*Crocuta crocuta*:) adult natal males that exhibit more aggression than immigrants have lower T levels (Holekamp and Smale, 1998). Additionally, these aggressive natal males are not preferred by resident females (Holekamp and Smale, 1998) and thus are presumably not breeding. Furthermore, hyena males attempting to join target clans after a dispersal phase possess decreased T levels (van Jaarsveld and Skinner, 1991). If low T levels are coupled with stressful situations, like the impending arrival of protective parents or high ranking males (in hyenas; van Jaarsveld and Skinner, 1991), individuals may show high levels of aggression. This hypothesis is consistent with our data, as well as the results from hyenas. Indeed, CORT showed the opposite pattern to T, being elevated in NAVs compared to non-NAVs. CORT levels may rise as (1) a consequence of stressful interactions with the chick or a returning parent. Alternatively, elevated CORT levels in NAVs could indicate (2) an anticipatory preparation for expected stressful stimuli (Ramade and Baylé, 1986). For NAVs, the impending return of a protective parent to the nest may be stressful. These two hypotheses are not mutually exclusive, and the relative contribution of each factor to elevated CORT levels can be tested in future experiments.

It is currently unclear if the observed differences in steroid levels between the two behavioral phenotypes are the only mechanistic explanation for NAV behavior. For

example, it is possible that hormonal changes early in ontogeny may cause permanent changes in an individual phenotype, organizing individuals into NAV or non-NAV phenotypes. A similar situation has been found in male tree lizards, which show permanent differences in sexual phenotype and behavior (for discussion, see Moore et al., 1998). This hypothesis could explain why we did not find differences in T levels among NAVs with increasing aggression levels. It is entirely possible to analyze hormone changes in ontogeny that may organize NAV behavior.

It is presently unclear whether and, if so, what ultimate reasons exist for NAV behavior. It is conceivable that NAVs may gain better nest sites, e.g., through acquisition of sites where nestings die after attacks, or that NAVs practice courtship or create future breeding opportunities by killing chicks deliberately. It remains a challenge for future research to find an adaptive explanation for NAV behavior, or to explain how it evolved as a by-product of other behaviors.

Acknowledgments

This study would have been impossible without the field assistance of Jason Schoch. We also thank the Galápagos National Park Service, the Charles Darwin Research Station, and TAME Airline for enabling this work. M. Hau and L. Martin provided comments improving previous versions of the manuscript and Peter Kappes and Stephanie Morgan provided additional help in the field. This is contribution no. 504 of the Charles-Darwin-Foundation and was supported by funds from Sigma Xi, the University of Illinois, Princeton University, and National Science Foundation grant DEB 9806606 to D.J.A.

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